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Reef fish community structure: an experimental study using small artificial reefs in Barkley Sound, British Columbia

by

© Dominique Gascon

A THESIS

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Date 23 April 1982

Abstract

Using small artificial reefs made of cement blocks, a community of shallow water reef fishes was experimentally studied in Barkley Sound (British Columbia) to examine the structuring mechanisms in this assemblage. The community under study inhabited a shallow reef made of rock boulders. The abundance of fish fluctuated with the seasons. The species diversity of this fish community was low (H' = 0.3–1.0), one species (*Coryphopterus nicholsi*) comprising more than 80% of the individuals present. Four species of rockfishes (*Sebastes caurinus, S. maliger, S. melanops,* and *S. pinniger*) and three species of benthic fishes (*Hexagrammos decagrammus, Jordania zonope,* and *Artedius spp.*) were also common. Experimental communities were established on ten identical artificial reefs made of cement blocks. Two series of reefs, built six months apart on sand 10 m away from the natural reef, tested the effects of seasons on community development. A third series, built in direct contact with the natural reef, examined the effects of distance and isolation on community development. In each series, a species equilibrium (approximately 6 species) was reached within six months. The specific composition of the artificial reefs was similar to that of the natural reef, although species other than *Coryphopterus nicholsi* were more abundant. Both juveniles and adults of all species were present, except for the rockfishes, which were represented only by young individuals. Tagging indicated that the benthic species remained permanently on the reefs, whereas a yearly turnover in rockfishes occurred. The intensity of interactions between species was estimated by measuring shifts in habitat use on the artificial reefs. Only *Sebastes melanops* showed consistent shifts in its space use in response to changes in the density of other species. Only two of these shifts appeared to be the result of interspecific competition. Interactions between species, with the exception of *S. melanops* had little effect on the spatial distribution of fish within the reefs. I examined the significance of the patterns of similarity between communities inhabiting identical habitats. High similarity values are usually interpreted as indicating the equilibrium status – that is communities structured primarily by interspecific competition. – of a community, whereas low values are usually interpreted in the opposite direction – i.e. non-equilibrium communities structured by mechanisms other than interspecific competition (mostly stochastic events). This was tested using a

randomization test. The null hypothesis of the test was that random colonization from the surrounding habitats was sufficient to explain the community structure on the artificial reefs. Six additional reefs (one third the original size) were built to test the effects of habitat size on community structure. The observed values on the reefs did not differ significantly from the null values, indicating that mechanisms, such as competition, were not required to explain the structure of the community. Habitat size had a strong effect, and the interpretations of previous studies were re-examined in light of this finding.

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I. INTRODUCTION

The ecology of reef fish communities has received a great deal of attention in recent years (Helfman, 1978a; Sale, 1980b), although most of this work has been limited to coral reef environments. By comparison, our knowledge of the ecology of more northerly communities is much more limited, most of the work being limited to southern California (eg. Bray and Ebeling, 1975; Hobson and Chess, 1976; Ebeling *et al.*, 1980), and the interpretation of these communities is usually done by extrapolating from the results obtained in tropical waters (eg. Stephens and Zerba, 1981).

In this study, I examined an assemblage of fish inhabiting a shallow rock rubble reef in Barkley Sound, British Columbia by following the development of the fish communities on small artificial reefs made of concrete blocks. Colonization studies form an important part of community ecology (Schoener, 1974a, 1974b; Sale and Dybdahl, 1975, 1978; Molles, 1978; Talbot *et al.*, 1978; Bohnsack and Talbot, 1980) as they allow one to follow the establishment of the structuring mechanisms with community development.

Small artificial reefs have been used frequently in the studies of reef fishes as they present great advantages over natural habitats. First, they guarantee that colonization will start on absolutely empty habitat patches, a fact that can rarely be ascertained in defaunation work (eg. Gunderman and Popper, 1975; Smith and Tyler, 1975; Sale *et al.*, 1980). Second, the habitat and microhabitat variables can be fully controlled. Microhabitat is known to be important in controlling fish community composition (Gosline, 1965; Izkowitz, 1977; Robertson and Lassig, 1980; Gladfelter *et al.*, 1980), and it is usually difficult to distinguish the role of habitat from that of biological variables in studies performed on natural habitats. Finally, because of the great structural simplicity of such artificial structures, which are made of well defined, discrete types of microhabitat, it is possible to quantify accurately the microhabitat requirements of the species present.

In this thesis, I examined specifically two points. First, I examined the community development on these artificial habitats and how this experimental system relates to the natural habitat. Obviously, the biological patterns on the artificial reefs is of little interest, unless it can be applied to the natural environment. The fish

community of the nearby natural reefs (rock rubble slope) is examined in chapter III. In chapter IV, I describe in detail the community found on the reefs, concentrating on the colonization process. Previous studies using artificial reefs were done in the relatively aseasonal tropical (Russell *et al.*, 1974; Talbot *et al.*, 1978; Bohnsack and Talbot, 1980) or subtropical (Molles, 1978) waters. Barkley Sound is markedly seasonal, and I examined the effects of this seasonality on community development and on the colonization by the species. Finally, I looked in detail at the spatial distribution of the fish on the artificial reefs and at the microhabitat selection. Resource separation is an important mechanism which may allow species coexistence (Schoener, 1974), and space is the dimension along which this separation is most likely to occur in reef fish, either as a direct object of competition (Sale, 1980b) or as an indirect object for resources associated with it – eg. food (Werner and Hall, 1976), shelter, or spawning sites.

In recent years, a controversy has arisen regarding the structuring mechanisms operating in reef fish communities (Helfman, 1978a). Some maintain that interspecific competition is one of the major mechanisms responsible for the structure of coral reef communities (Smith and Tyler, 1972, 1975; Gladfelter *et al.*, 1980; Anderson *et al.*, 1981) whereas others claim that its role is relatively minor, with other factors (eg. chance recruitment) being supposedly more important (Sale and Dybdahl, 1975; Talbot *et al.*, 1978; Bohnsack and Talbot, 1980; Stephens and Zerba, 1981).

The second point I looked at is the importance of interspecific competition on the structure of the reef fish community, i.e. which species will be present, and in what numbers. By carefully designing the artificial habitats, it is possible to control the most important biological factors (eg. dispersal, habitat selection, etc.) that may affect community composition. I tested the following general hypothesis on the role of competition in this system: that the presence and abundance of species is in part the result of competition between them. As a structuring mechanism, competition would create some orderly patterns of distribution and abundance, while in non-competitive communities, the fish assemblages on the reefs would be merely a random sample of dispersing fish from the natural habitat. The testing of this general hypothesis is required before more specific questions may be usefully asked on the competitive

mechanisms between pairs of species (eg. Hixon, 1980; Larson, 1980a).

Following this introduction, I review the recent literature on reef fish community structure; I shall also briefly review the use of artificial reefs and the life history of the species present in the habitat under study. Materials of chapters II and III were published in Gascon and Miller (1981, 1982).

A. Literature review

Reef fish community structure

In recent years, a great deal of attention has been given to the ecology of reef fishes (Sale, 1977; Dale, 1978; Helfman, 1978b; Smith, 1978a, 1978b; Talbot *et al.*, 1978; Gladfelter *et al.*, 1980; Robertson and Lassig, 1980; Waldner and Robertson, 1980; Anderson *et al.*, 1981; Ogden and Ebersole, 1981; Stephens and Zerba, 1981). This recent interest has been sparked in great part by the development of Sale's lottery hypothesis (Sale, 1975, 1976, 1977, 1978a, 1978b, 1979, 1980a; Sale and Dybdahl, 1975, 1978; Sale *et al.*, 1980). Coexistence of coral reef fishes has usually been thought to be achieved through fine resource separation mediated by interspecific competition (Smith and Tyler, 1972, 1973a, 1973b, 1975) [the so-called equilibrium communities[1] – Connell, 1978], whereas the lottery hypothesis emphasizes stochastic events. I will review here the results of this work on coral reef communities, starting with the lottery hypothesis which has stimulated much of this work.

The lottery hypothesis is based on four principal assumptions (Sale, 1977, 1980a; Robertson and Lassig, 1980):

1. Most species of reef fish are territorial or hold some space on the reefs; living space in thus assumed to be in limited supply and to be the object of intense competition.
2. There is no strong competitive hierarchy (and no niche separation) in guilds

[1]This is an unfortunate use of terms; the words equilibrium and non-equilibrium have been used independently of whether or not population numbers were stable. By the use of these terms, it is normally meant that equilibrium communities are structured primarily through interspecific competition, whereas non-equilibrium communities are structured otherwise. This notation should be abandoned as it is needlessly vague and confusing.

(groups of species with similar ecological requirements [Root, 1967]) of demersal species; the prior resident effect is of prime importance in determining the success of competitive encounters.

3. There is a fairly constant "oversupply" of planktonic recruits, which is relatively independent of adult stock.

4. Chance alone determines which member of a guild will occupy a vacant patch.

The larval planktonic and adult demersal phases of the life cycle are considered to be relatively independent of each other, and the factors influencing one bear little impact on the success of the other. Thus, a lower ranked adult competitor would never be excluded, as it would re-enter the lottery as an equal through its planktonic phase. This is a convenient loophole in the model, as some of the most interesting phenomena are hidden in the planktonic stage, which is notoriously difficult to study.

Sale (1975, 1976, 1978a, 1980) has attempted to demonstrate the stochastic nature of settlement and the absence of competitive hierarchy (points 2 and 4) with a series of removal experiments. He was able to show that the reallocation of vacated territories among the members of a guild was random (i.e. independent of prior resident and abundance of species in a patch), supporting the idea that the species had equal chances of invading the community. The use of space was constant (i.e. the territories were all constantly occupied [Sale, 1978b]), suggesting that it was in limited supply, although Robertson and Sheldon (1979), Williams (1980), and Robertson *et al.* (1981) have provided strong evidence to the contrary. If this last result were to be general, it would invalidate one of the major assumptions of the model. The remaining assumption (point 3: oversupply of recruits) has never been examined; it may be untestable. It is based on the weak relationship between stock and recruitment in temporal stocks (Cushing, 1975), that is the numbers of recruits are relatively independent of the adult population size.

In another set of experiments, Sale and Dybdahl (1975, 1978) have attempted to show that the high degree of small scale variability in community structure was the result of purely stochastic events. They compared communities developing on two series of homogeneous coral heads with communities developing at successive intervals on each of these coral heads. They predicted that if they were microhabitat

specialists, the same species – or set of species – would re-invade consistently the same coral head over the successive censuses. In their analysis, they considered the different patches as being distinct sets of resources, and not as being replicates of one type of habitat resource. They were unable to detect such selection, from which they concluded that the fish were habitat generalists settling randomly on these habitat patches; they rejected the hypothesis that coexistence of these species was the result of the niche separation of the habitat resources. Several points that they have neglected may somewhat alter their conclusions:

1. The small size of their habitat patches (mean no. fish/patch = 6.8) and the large number of species involved (56) would have produced only a large degree of variability between patches, as only a few of these species were present on each patch.
2. The apparent lack of habitat selection by the fish may have been a result of their design. Their patches were extremely homogeneous and the microhabitat differences between them perhaps too small for the fish to detect, thus disallowing niche separation on the habitat (i.e. patch) dimension. When they used two types of coral heads (live and dead), selection did occur between them, contradicting their conclusion.
3. The most serious criticism is that their experiment required a great deal of temporal stability. By comparing settlement on constant microhabitats (the same patch over time) with the settlement on different microhabitats (the different patches at one time), they rejected the hypothesis that fish were selecting microhabitats. However, changes in their habitat patches over time (that they acknowledged) and changes in the available recruits (Russell *et al.*, 1977) invalidated their comparison. Because of this lack of temporal constancy, it is impossible to distinguish their interpretation (random settlement by generalist species) from the alternate hypothesis (tracking by specialists of a constantly changing environment).

Russell *et al.* (1974) and Talbot *et al.* (1978) have also looked at the colonization process on small artificial reefs on the Great Barrier Reef of Australia and considered it mostly stochastic. They attributed the apparent unpredictability in

community development to disturbances and predation pressure, in accordance with Connell's intermediate disturbance hypothesis, but nowhere did they present firm evidence on what those disturbances might be. Bonhsack and Talbot (1980) compared the colonization on those reefs to that of similar ones built in Florida (species pool > 1000 vs species pool > 500). Species packing (measured as a mean no. of species/reef) was not greater in Australia than in Florida, indicating that the greater species richness of Australian reefs was not a result of finer niche subdivision, supporting one of Sale's points (no. 2).

Finally, Chesson and Warner (1981) have examined the mathematical stability of lottery systems. Such systems are usually unstable, except for a small range of conditions. They also found that environmental variability would enhance stability and favour coexistence, but the modified model is then hardly distinguishable from the intermediate disturbance hypothesis (Connell, 1978).

Critics of the stochastic view of community structure in general and of the lottery hypothesis in particular have recently appeared; they concentrate on two major aspects:

1. Anderson *et al.* (1981), Fricke (1977), Itzkowitz (1977) and Waldner and Robertson (1980) have looked at guilds of reef fishes and they have all reported large degrees of habitat segregation, which appeared sufficient to explain the coexistence of the members of these guilds. Anderson *et al.* (1981) have shown that among the Chaetodontidae of the Great Barrier Reef, species with similar ecological requirements never co-occurred along a transect ranging from the Australian coast to the outer reefs, and that co-occurring species could always be ecologically separated. Robertson and Lassig (1980) have re-examined Sale's (1974b) community of Pomacentridae and found greater degree of niche separation than Sale had originally reported. Dale (1978) suggested that the lottery hypothesis was only a special case, which could explain coexistence in the narrow zone of overlap between the exclusive habitat zones used by the guild members.

   The demonstration of niche separation is not a demonstration of competitive exclusion (Wiens, 1977). Experimental work on competition has

yielded only conflicting results. Sale's removal experiments failed to detect strong competitive effects, although the scale at which he was working was perhaps too small to detect them (Anderson *et al.*, 1981). Robertson and Sheldon (1979) were unable to detect competition for shelters between two species of Panamanian reef fishes. To be significant, competition requires that some resource be in limited supply. It is worthwhile to mention again the results of Robertson *et al.* (1981) and Williams (1980), who indicated that space may not be limiting; under these circumstances, competition would be only a weak force. On the contrary, Hixon (1980) and Larson (1980a), working on temperate reefs, have shown that interspecific competition could sharply limit the distribution of some species in groups of close congeners.

2. Non-equilibrial (i.e., in which interspecific competition is not considered important) approaches to community structure have emphasized the apparent lack of predictability (equated with lack of stability) of community development (Sale and Dybdahl, 1975, 1978; Talbot *et al.*, 1978), whereas the more deterministic hypotheses predict that stable equilibrial conditions will develop. Many authors have recently looked at the stability and predictability of fish assemblages on coral reef patches (Anderson *et al.*, 1981; Brock *et al.*, 1979; Gladfelter *et al.*, 1980; Gunderman and Popper, 1975). They all looked at relatively large patches (100 to > 1000 m^2) and they all reported that the fish assemblages on these patches were stable and predictable. Ogden and Ebersole (1981) re-examined Randall's (1963) artificial reef and found that its community structure remained remarkably constant in the intervening 17 years.

These conflicting interpretations appear to be scale-related; Sale (1980b) and Anderson *et al.* (1981) have both commented on the point with opposing – but not entirely exclusive – views. Authors who claimed that communities were "predictable" worked on systems several orders of magnitude larger than those who claimed that they were not. Communities structured through purely stochastic events on a small scale, would converge to some average (i.e. equilibrium) by the action of the central limit theorem (Sale, 1980b), when examined on a larger scale, without the need of any underlying process. On the other hand, Anderson *et al.* (1981) have pointed out that

the scale at which some of these studies have been performed (eg. Sale and Dybdahl, 1975, 1978; Talbot *et al.*, 1978) is too small to detect population dynamics phenomena like competition (which would affect population size), thus the apparent stochasticity is the result of small-scale noise irrelevant to the dynamics of the much larger systems. Most reef fish species produce pelagic planktonic larvae that can disperse over several km, possibly several hundreds of km (Barlow, 1981), so it seems unlikely that looking at systems smaller than 100's of m^2 is sufficient to detect the dynamics of these fish populations.

This controversy is then probably more the result of the different sample sizes used (i.e. convergence towards an average with greater sample size) rather than different processes operating on different scales (as both are too small to represent the dynamics of these populations accurately). It comes from a lack of definition of predictibility and stability (see Sutherland, 1981), which has been left so far to the good biological sense of the investigator; highly variable (but small) systems may be structured by basically deterministic processes (eg. competition), the high variance resulting from the small sample size, whereas the opposite is also true. This lack of precision does not provide any means of determining if some processes are at work in these systems. Simberloff (1978) provides the criteria required to determine whether deterministic or only stochastic processes are required to explain assemblages of species. They urgently need to be applied to reef fish communities.

Artificial structures in the marine environment

Artificial reefs have been widely used throughout the world to attract fish and enhance local fisheries (Carlisle *et al.*, 1964; Scarrat, 1968; Turner *et al.*, 1969; Dewees and Gotshall, 1974; Briggs, 1975; Silva Lee, 1975; Chang *et al.*, 1977; Hirose *et al.*, 1977; Higo and Nagishima, 1978; Okamoto *et al.*, 1979). These efforts have been reviewed by Stone (1978) and Stroud (1980). Steimle and Stone (1973) provided an exhaustive bibliography on the subject up to 1972. These studies have demonstrated that artificial reefs can dramatically increase the density of reef fishes; in all cases the authors were mainly concerned with demonstrating the attractiveness of the reefs and to perform cost-benefit analysis.

Very few studies have attempted to investigate the factors responsible for attracting fish to reefs. Ogawa and coworkers published a series of papers, fortunately with English abstracts, (Ogawa, 1966, 1967, 1968; Ogawa and Aoyama, 1966; Ogawa and Onoda, 1966; Ogawa and Takemura, 1966a, 1966b; Ogawa *et al.*, 1977), attempting to determine which habitat characteristics were responsible for attracting fish to reefs.

On a smaller scale, artificial structures have been used as experimental tools. Randall (1963) constructed a small reef of cement blocks in the U. S. Virgin Islands. The density of fish on that reef was 11 times that of natural reefs. Ogden and Ebersole (1981) re-examined it 14-17 years later and found that the community had remained remarkably constant during that period. Russell *et al.* (1974), Talbot *et al.* (1978), and Bohnsack and Talbot (1980) have built small reefs of cement blocks to investigate the structure of coral reef fish communities; their studies were discussed in detail in the previous section

Bohnsack (1979) and Molles (1978), in Florida and the Gulf of California respectively, have also built small reefs of cement blocks to test the predictions of the Theory of Island Biogeography (MacArthur and Wilson, 1967). They reported equilibrium values and turnover rates consistent with the theory. Bohnsack (1979) also found that the equilibrium number of fish species decreased with distance from the source of colonists, as predicted. Both he and Molles (1978) found that the structural complexity of the reefs had little effect on the species equilibrium and number. Talbot *et al.* (1978) reported similar findings from Australia.

The ecology of northeast Pacific fishes

Moulton (1977) has recently reviewed the ecology of these fishes, and in this section I shall update this and present the pertinent life history information on the species commonly encountered in this study.

Contrary to those of coral reefs, temperate reef fish communities are poorly known and understood. Most of the work so far has been descriptive and was performed in the faunistically intermediate area of southern California (Quast, 1968a). Alevizon (1975a, 1975b). Bray and Ebeling (1975), Ebeling *et al.* (1980), Hallacher (1977), Hobson and Chess (1976), Love and Ebeling (1978), and Stephens *et al.*

(1970) have examined the structure of the reef/kelp forest fish community of Southern California and have discussed the mode of resource separation among its members. Ebeling and Bray (1976) have examined the diel activity of these fish which is much less rigid than that of their tropical counterparts. Quast (1968b, 1968c), Miller and Geibel (1973), and Feder *et al.* (1974) provided additional information on the ecology of this community.

Recently, some experimental work on the mechanisms of coexistence was done in the same area. Larson (1980a, 1980b) looked at the bathymetric separation between two territorial rockfishes (*Sebastes chrysomelas* and *S. carnatus*) using reciprocal removal experiments. The deeper species, *S. carnatus*, extended its range into shallow water when *S. chrysomelas* was removed. The downward movement of *S. chrysomelas* was minimal in the alternate experiment, from which it was concluded that *S. chrysomelas* competitively excluded *S. carnatus* from shallow water. Hixon (1980) performed a similar experiment on seaperches (*Embiotoca spp.*), with essentially the same results.

Information on the ecology of more northern communities is almost entirely lacking. Moulton (1977) conducted the only study of these fish in Puget Sound. He looked at seasonal changes in density and distribution, food, growth, and other life history parameters of the major species of the nearshore community. Leaman (1980) provided additional information on the species found in Barkley Sound. Marliave (1975) described the larval biology and settlement behaviour of many Barkley Sound species.

Life history information on individual species is more abundant, although it is almost exclusively limited to rockfish (*Sebastes spp.*). Rockfish are a very large group (68 species on the west coast of North America [Chen, 1974]) which can be divided into essentially open-water species (eg. *S. flavidus, S. melanops, S. pinniger*) and demersal species (eg. *S. auriculatus, S. caurinus, S. maliger, S. nebulosus*) (Hallacher, 1974). Growth of these inshore species is fairly rapid, as they reach 15 to 20 cm by three years of age (Boehlert and Kapperman, 1980; Leaman, 1976; Moulton, 1977; Patten, 1973; Phillips, 1964; Six and Horton, 1977), although it is somewhat faster for the open-water species, (Moulton, 1977). Their maximum reported sizes are around

60 cm, with maximum ages of 20 to 25 years. Patten (1973) found that all 4-year-old *S. caurinus* from Puget Sound were sexually mature, and although the information is lacking for the other species, it is presumably similar (Love and Westphal, 1981).

Sebastes spp. are ovoviviparous, the females retaining the eggs until hatching (Hart, 1973). Reproduction time is variable among the species of *Sebastes* (Hitz, 1962; Westerheim, 1975). *S. melanops* is the first to spawn, its planktonic larvae having been collected off Oregon between April and June (Laroche and Richardson, 1980), at which time they presumably settled on the bottom (Leaman, 1976). Larvae of *S. pinniger* were collected between March and June, whereas the demersal juveniles were obtained in July and August (Richardson and Laroche, 1979). Parturition of *S. caurinus* occurs in April (Delacy *et al*. 1964; Huekel, 1980; Moulton, 1977; Miller and Geibel, 1973). Ontogenetic changes in habitat requirements occur in some species which move into deeper water as they grow (Leaman, 1976). Some of the open-water species also show daily short range migrations between home site and feeding habitat (Carlson and Barr, 1977; Leaman, 1976; McElderry, 1979). The studies of Leaman (1976) and McElderry (1979) are especially pertinent to my study as they looked at the Barkley Sound population of *S. melanops*. The food of rockfish was studied by Hueckel (1980), Leaman (1976), Moulton (1977), Patten (1973), Phillips (1964), Prince (1975), and Prince and Gotshall (1976). All agree that these species have essentially similar diet, preying upon crustaceans and small fish (clupeoids). The proportion of fish in the diet increases with increase in size. The open-water species normally take prey in midwater (eg. macrozooplankton) whereas the demersal species prey on benthic animals (eg. crabs).

Information on the life histories of other species is scarce. Leaman (1980) and Moulton (1977) have described growth and food habits of *Hexagrammos decagrammus*; it is a generalized benthic predator feeding on almost any suitably sized animal. Moulton (1977) has also found that males and females, which are dichromatic, showed partial bathymetric separation, the males being found slightly deeper (3 m) than the females. Leaman (1980) added that they are territorial, without providing firm evidence.

The life history of the goby, *Coryphopterus nicholsi*, was studied by Ebert and Turner (1962) and Wiley (1973). It feeds primarily on small crustaceans (amphipods, isopods, etc.) (Leaman, 1980; Wiley, 1973). Ebeling and Bray (1976) reported that it was exclusively diurnal. K.S. Cole (U. of A.) is presently doing an intensive study of its population structure and territorial behaviour in Barkley Sound. Useful information on other species (*Jordania zonope, Artedius spp.*), apart from some anecdotal comments, is almost entirely lacking.

II. METHODS

This work was entirely performed by SCUBA diving. My diving partner in all cases, unless otherwise mentioned, was Roberta Miller who was present not only for safety reasons, but was actively involved in collecting and recording the data.

A. Study area

The study was conducted in the Ross Islets of Barkley Sound (48°52' N, 125°9' W), British Columbia. Barkley Sound is a large bay on the west coast of Vancouver Island (Fig. 1). Its oceanography and main biological communities have been described by Austin (1970), Austin *et al.* (1970), Lane (1962), and Leaman (1980).

Ross Islets Study Site

The study site was located in a narrow channel between two small islands (Fig. 1). All the work was done along the north shore of the largest of these islands. This area was always sheltered, even in the heaviest seas.

Along the shore of the island, there was a steep rock rubble slope (Plate I.1), descending to a sand bottom (Plate I.2), 5–6 m deep (at mean low water; mean water depth being approximately 2.2 m above MLW). The upper part of the slope was formed almost exclusively of medium sized (15–50 cm in diameter) rocks, whereas the bottom section was made of a mixture of rocks and sand. The sand bottom gradually sloped to the middle of the channel at a depth of 15–18 m. A narrow bed of the kelp *Macrocystis integrifolia* was present at the top of the rock rubble slope.

The mapping of the study area was done as follows: a marked weighted reference line (200 m long, marks every 5 m) was sunk parallel to the shoreline. A 10 m surveyor's chain was laid perpendicular to the reference line at each of the marks. Depth was measured with a capillary depth gauge (accurate to 0.25 m at those depths) along the length of the chain at regular intervals. After correcting for tide height (from the tables published from the Canadian Hydrographic Service) the horizontal distance between the line and the measured depth along the surveyor's chain could be easily obtained by simple trigonometric transformation.

The temperature was continously recorded at the study site with a Peabody–Ryan recording thermometer located on the bottom at a depth of 8 m. The

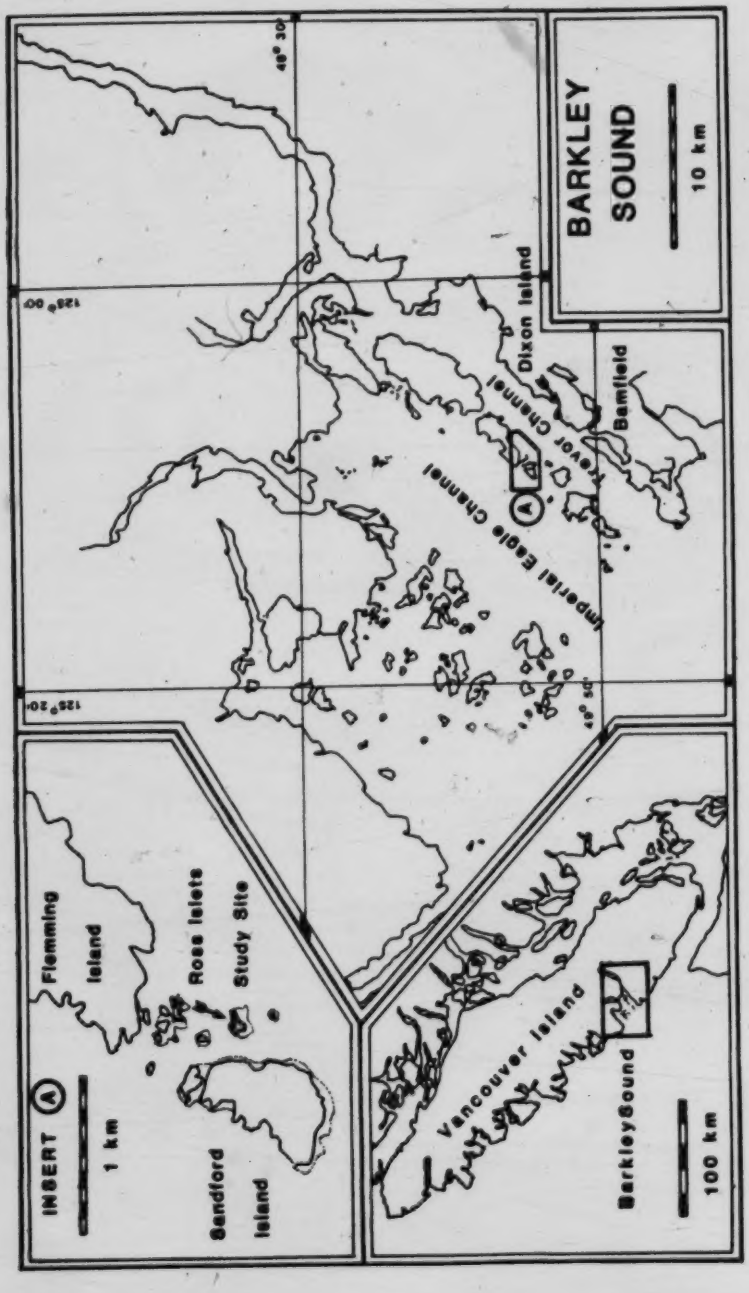

Figure 1: Map of Barkley Sound. Insert A is an enlargement of the study area in the Ross Islets.

Plate I: Underwater views of the habitat of the Ross Islets and of the artificial reefs.
1: Rock rubble slope; the fish is *Sebastes maliger*.
2: The sand habitat at the base of the rock rubble slope in mid-summer. The fish is *Hydrolagus colliei*.
3: A small insular reef, reef number 17 in March 1980.
4: An insular reef, reef number 6 in March 1980.

1
2
3
4

temperature varied from 14° in summer to 6° in winter (Fig. 2). Water visibility (defined as the maximum distance at which reefs could be seen) was also noted (Fig. 2). The visibility was at its minimum in the summer (3–4m) and highest in winter (to at least 10 m). Marked reduction in visibility followed the frequent winter storms. The tidal range in Barkley Sound averages 2.8 m (maximum 4.1, min. 0.8).

The algal community at the study site was dominated by *Macrocystis integrifolia*, which formed a dense bed at the top of the rock rubble slope. The phaeophyte *Desmerestia ligulata* was also very abundant, forming a narrow band just below the *Macrocystis* bed. The extent of the cover of *Desmerestia* varied annually, reaching a maximum in 1980, when it almost reached the sand bottom in some areas. In deeper waters, *Nereocystis luetkeana, Costaria costata, Laminaria spp., Porphyra spp.*, and *Agarum spp.* were also common.

The most common macro-invertebrates on the rock rubble area were the cnidarians *Balanophylla elegans, Tealia spp.* and *Metridium senile*, the echinoderms *Cucumaria miniata, Solaster stimpsoni, Strongylocentrotus franciscanus*, and *S. droebachiensis*, the abalone *Haliotis kamtschatkana*, the scallop *Hinnites giganteus*, the octopus *Octopus dofleini* and the crabs *Pugettia producta* and *Cancer productus*. On the sand, the burrowing anemone, *Pachycerianthus fimbriatus*, the seapen *Ptilosarcus gurneyi*, the nudibranch *Dendronotus iris*, the moonsnail *Polinices lewisii*, the clams *Protothaca (staminea), Tresus (nuttallii)*, the echinoderms *Pisaster brevispinus, Pycnopodia helianthoides*, and *Parastichopus californicus* (the latter two being also present on the rocks) were all abundant. The solitary ascidian *Cnemidocarpa finmarkiensis* was also noticeable. In addition to the demersal species of fish, the following pelagic species were also common *Squalus acanthias, Clupea harengus pallasi, Engraulis mordax*, and *Oncorhynchus spp.*, their presence being known from some preliminary netting at the study site.

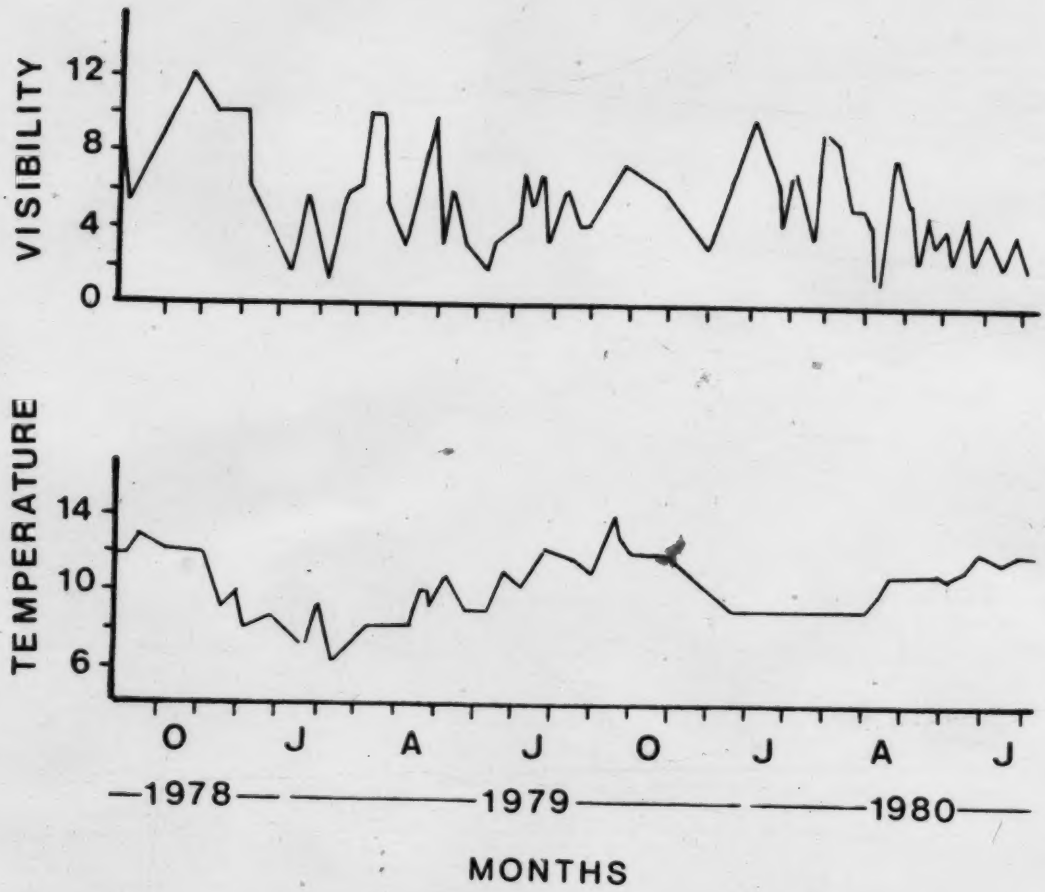

Figure 2: Seasonal changes in temperature and visibility at the study site. Visibility (in metres) above; Temperature (in °C) below.

B. Material and methods

Artificial reefs

Ten identical artificial reefs (Fig. 3, Plate I.3) were originally constructed of standard concrete construction blocks. The reefs were terraced structures arranged in 3 rows. Three types of concrete blocks, grouped into units of constant volume (40 x 30 x 20 cm) alternated both horizontally and vertically. Four sizes of openings were found: units made of small blocks had 9 small holes (9.3 x 3.6 cm); units made of medium blocks had 4 medium holes (14 x 8 cm); and units made of large blocks had one large hole (18 x 21 cm) and one vertical hole (18 x 6 cm). The reefs were assembled underwater directly on the sand, and gaps were present between the rows (horizontal holes) and the columns (vertical holes). No mortar was used, but sessile organisms cemented the blocks together in a matter of months.

All the holes were theoretically open-ended; however the construction of the reefs directly on the sand caused some misalignments, blocking the smaller holes in the wider section at the base of the reefs. Therefore, small, medium, and vertical holes in the bottom row, and the small holes in the centre row were considered closed, creating separate shelters on either side. The number of resource types (i.e. shelter types with which the fish are associated) can then be easily quantified; their relative availability, in relation to elevation is given in Table 1.

The reefs were organized in a linear fashion along a rock rubble slope (Fig. 4) in a narrow channel between two small islands. Reefs 1 to 6 (called insular reefs) were located 10 m from the rock rubble slope, with the exception of reef no. 1 which was mistakenly built at only 7 m from the rocks. The remaining reefs (number 7 to 10, called continental reefs) were positioned in direct contact with the rock rubble slope to assess the importance of the 10 m distance to the insular reefs as a barrier to colonization. The minimum distance between reefs was 10 m, insuring effective visual isolation, since the water visibility normally does not exceed 10 m at the study site. Not once while diving on a reef, could the next one be seen. A guide line, passing the reefs at some distance was used to aid the divers in times of low water visibility. Since it became rapidly covered by epiphytic growth and was often buried underneath large brown algae, the line was inconspicuous and it could not have

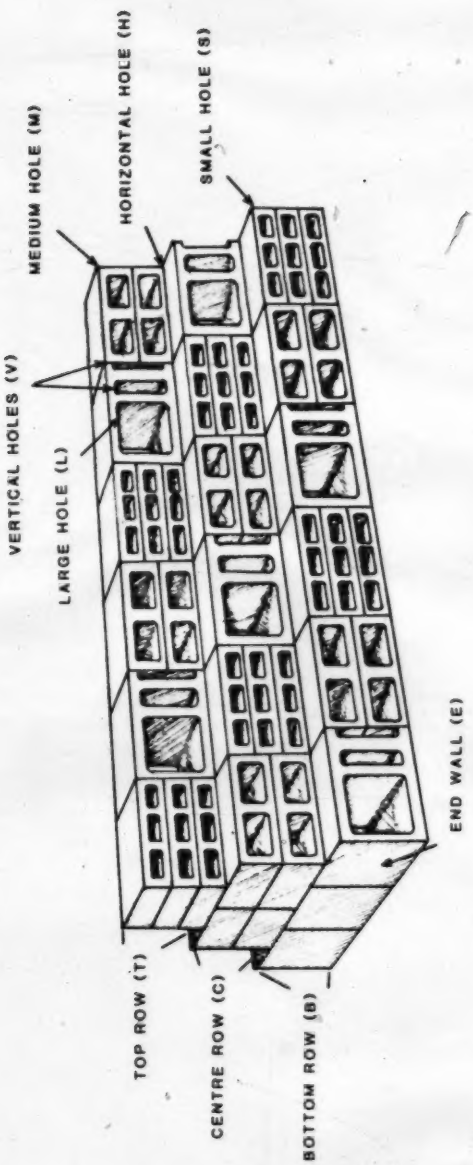

Figure 3: Diagram of the artificial reefs. The dimensions are 2.4 m long, 0.6 m basal width, and 0.9 m high.

Table 1: Numbers of the different types of opening with respect to row of the artificial reefs. Holes marked with an asterisks are closed at one end due to the misalignment of the blocks. The narrow holes of the large blocks are combined with the vertical holes (between columns).

ROW	Bottom	Centre	Top
HOLE TYPE			
Large	2	2	2
Medium	16*	8	8
Small	36*	36*	18
Horizontal	12*	12*	6*
Vertical	14*	7	7
End Walls	3	2	1

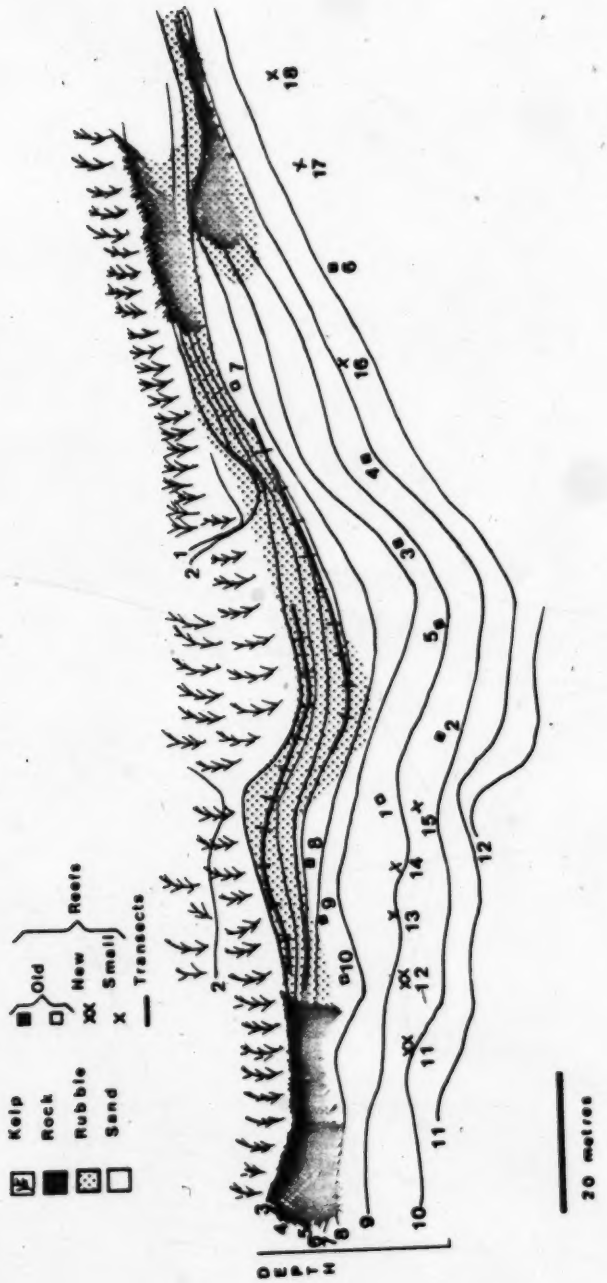

Figure 4: Bathymetric map of the study site. The depth contours (light lines) are in metres. The squares mark the position of the artificial reefs. The position of the transects is also indicated.

been used as a guide by the fish to swim from reef to reef.

Winter reefs (no. 1 to 4) were constructed in February 1978, while the six summer reefs (no. 5 to 10) were built in August 1978. Therefore there were 4 winter insular reefs (no.1 to 4), 2 summer insular reefs (no. 5 and 6) and 4 (summer) continental reefs (no. 7 to 10). Originally, it was not planned to construct continental reefs, but they were added after it was realized that most of colonists were large fish, presumably coming from the rock rubble, and not planktonic recruits (as in tropical waters). The length of the rock rubble slope did not allow me to install more than ten reefs without introducing additional variables in the system such as:

1. possible loss of independence of the reefs by building them closer together;
2. habitat heterogeneity by constructing the remaining reefs in different areas;
3. possibility of a stepping stone effect by building additional reefs behind the continental reefs.

In January 1980, reefs no. 1, 7, and 10 were dismantled in order to make room for different structures. Eight additional reefs were built in February 1980. Two new insular reefs (called new insulars, nos. 11 and 12) identical in every respect to the original reefs, were built to serve as controls for new reefs to be built. Reef no. 11 was built from new blocks, whereas reef no. 12 was built from blocks salvaged from reef no 10.

Six smaller reefs (number 13 to 18, called small reefs) were built at the same time (Fig. 5, Plate I.4). They were similar to the standard units, except for their size which was exactly one third of the original one (two columns instead of six). These reefs were also built from blocks salvaged from the demolition of older reefs (reefs no. 13 to 15, blocks from reef no. 1; reefs 16 to 18, blocks from reef no. 7). Thus, with the exception of reef no. 11, all reefs, new and old were made of blocks of the same biological age.

In order to position five additional reefs (8 new ones minus the 3 dismantled), the rigid criteria set up at the beginning had to be modified (Fig. 4). The additional row of small and new reefs was positioned behind the existing line of continental reefs. Furthermore, reef no. 11 on the one hand, and reefs no. 17 and 18 on the other were added respectively at the far eastern end and far western end of the reef

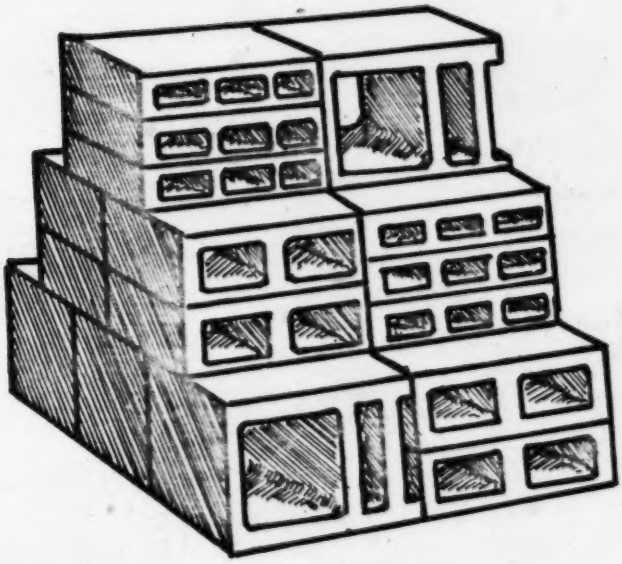

Figure 5: Diagram of the small artificial reefs. The overall dimensions are 0.8 m long, basal width 0.6 m, and 0.9 m high.

line, just beyond the edges of the homogeneous habitat of the study site. Differences in habitat were more noticeable at the west end of the line (reefs no. 17 and 18) where the water was slightly deeper (10–12 m instead of 8–10 m for the rest of the study site). The minimum distance of 10 m between reefs was not changed.

Data collection

Fifty-four visual censuses of the fish populations inhabiting the reefs (41 for the summer reefs) were conducted using SCUBA between February 1978 and August 1980. The surveys were conducted at two-week intervals, except on a few occasions owing to stormy weather. As a normal practice, two or three dives were done on consecutive days to complete a census, except on seven occasions, when the interval ranged from two to five days, the delays being caused again by stormy weather. The detailed sampling schedule is given in Table 2.

Two divers, R. Miller and I, made each census. Exceptionally, when one of us was unable to dive, a census was conducted by one person only, since there was nobody else competent to identify fishes.

The reef censuses were conducted as follows. The two divers approached a reef from opposite sides and recorded all fish visible in front and outside the structure. Then all holes were carefully examined for fish. The position of each fish seen (row, column, block type, hole) and their estimated total length were recorded. The length estimations were always done by comparison with structures of the reefs. Fish were put into length classes, 2 cm classes for fish estimated to be < 15 cm long, and 5 cm classes for those estimated to be > 15 cm. The divers then exchanged sides and repeated the procedure. There was little difficulty in recognizing an individual sighted by both divers, since most of the fish remained in the same position. After a dive, the observations were plotted on a diagram of the reefs, in order that a fish seen from both sides, or seen by both divers, was not counted twice. When only one of us was present, the two sides were censused entirely only once.

The original organization of the study site was maintained between surveys no. 1 to 39. As mentioned earlier, reefs no. 1, 7 and 10 were dismantled in January 1980 and they were not included in censuses beyond no. 37. Monitoring of the new

Table 2: Sampling schedule

Survey[1]	Dates	Reefs	Observers[2]
C	11/ 2/1978	3,4	
C	23/ 2/1978	1,2	
1	14/ 3/1978	1,2,3,4	G
2	4/ 4/1978	1,2,3,4	G
3	18/ 4/1978	1,2,3,4	G
4	2/ 5/1978	1,2,3,4	G
5	18/ 5/1978	1,2,3,4	G
6	30/ 5/1978	1,2,3,4	G,M
7	13/ 6/1978	1,2,4	G,M
	14/ 6/1978	3	G,M
8	26/ 6/1978	1,2,3,4	G,M
9	13/ 7/1978	1,2,3	G,M
	14/ 7/1978	4	G,M
10	25/ 7/1978	1,2,3	G,M
	26/ 7/1978	4	G,M
11	9/ 8/1978	1,2,3,4	G,M
12	24/ 8/1978	1,2,3,4	G,M
C	27/ 8/1978	7	
C	28/ 8/1978	6,8	
C	31/ 8/1978	9	
C	3/ 9/1978	10,5	
13	7/ 9/1978	1,2,5,8,9,10	G,M
	8/ 9/1978	3,4,6,7	G,M
14	22/ 9/1978	1	M
	23/ 9/1978	2,8,9,10	M
	25/ 9/1978	3,4,5,6,7	M
15	12/10/1978	1,2,8,9,10	M
	14/10/1978	3,4,5,6,7	M
16	30/10/1978	1,8,9,10	G,M
	31/10/1978	2,3,4,5,6	G,M
	1/11/1978	7	G,M
17	17/11/1978	1,8,9,10	G,M
	20/11/1978	2,3,4,5	G,M

Table 2: continued.

Survey[1]	Dates	Reefs	Observers[2]
18	1/12/1978	1,2,8,9,10	G,M
	5/12/1978	3,4,5,6,7	G,M
19	13/12/1978	1,2,3,4,5,6,7,8,9,10	G,M
20	18/ 1/1979	1,2,8,9,10	G,M
	19/ 1/1979	3,4,5,6	G,M
21	14/ 2/1979	1,2,8,9,10	G,M
	16/ 2/1979	3,4,5,7	G,M
	19/ 2/1979	6	G,M
22	27/ 2/1979	1,2,8,9,10	G,M
	28/ 2/1979	3,4,5,6,7	G,M
23	12/ 3/1979	1,2,8,9,10	G,M
	13/ 3/1979	3,4,5,6,7	G,M
24	26/ 3/1979	3,4,5,6,7	G,M
	27/ 3/1979	1,2,8,9,10	G,M
25	10/ 4/1979	1,2,8,9,10	G,M
	11/ 4/1979	3,4,5,6,7	G,M
26	24/ 4/1979	3,4,6,7	G,M
	25/ 4/1979	1,2,5,8,9,10	G,M
27	8/ 5/1979	1,2,8,9,10	G,M
	9/ 5/1979	3,4,5	G,M
	10/ 5/1979	6,7	G,M
28	24/ 5/1979	1,2,8,9,10	G,M
	25/ 5/1979	3,4,5,6,7	G,M
29	7/ 6/1979	1,2,8,9,10	G,M
	8/ 6/1979	3,4,5,6,7	G,M
30	20/ 6/1979	3,4,5,6,7	G,M
	21/ 6/1979	1,2,8,9,10	G,M
31	4/ 7/1979	3,4,5,6,7	G,M
	5/ 7/1979	1,2,8,9,10	G,M
32	19/ 7/1979	1,2,8,9,10	G,M
	20/ 7/1979	3,4,5,6,7	G,M
33	1/ 8/1979	3,4,5,6,7	G,M
	2/ 8/1979	1,2,8,9,10	G,M
34	15/ 8/1979	1,2,8,9,10	G,M
	16/ 8/1979	3,4,5,6,7	G,M

Table 2: continued.

Survey[1]	Dates	Reefs	Observers[2]
35	29/ 8/1979	3,4,5,6,7	G,M
	3/ 9/1979	1,2,8,9,10	G
36	27/ 9/1979	1,2,8,9,10	M
	28/ 9/1979	3,4,5,6,7	M
37	30/10/1979	1,2,8,9,10	M
	31/10/1979	3,4,5,6,7	M
38	6/12/1979	1,2,3,4,5,8,9,10	M
39	9/ 1/1980	3,4,5,6	G,M
	10/ 1/1980	1,2,8,9	G,M
40	24/ 1/1980	1,2,5,8,9	G,M
	25/ 1/1979	3,4,6	G,M
41	5/ 2/1980	3,5,6	G,M
	6/ 2/1980	1,2,8,9	G,M
42	26/ 2/1980	2,3,4,8,9	G,M
	27/ 2/1980	6	G,M
C	28/ 2/1980	16,17,18	
C	29/ 2/1980	13,14,15	
C	1/ 3/1980	12	
C	3/ 3/1980	11	
43	11/ 3/1980	4,6,16,17,18	G,M
	12/ 3/1980	2,3,5,8,9,11,12,13,14,15	G,M
44	24/ 3/1980	2,5,8,9,11,12,13,14,15	G,M
	25/ 3/1980	3,4,6,16,17,18	G,M
45	8/ 4/1980	2,5,8,9,11,12,13,14,15	G,M
	10/ 4/1980	3,4,6,16,17,18	G,M
46	22/ 4/1980	3,4,6,16,17,18	G,M
	23/ 4/1980	2,5,8,9,11,12,13,14	G,M
	25/ 4/1980	15	G,M
47	6/ 5/1980	2,3,4,5,6,8,9	
		11,12,13,14,15,16,17,18	G,M
48	21/ 5/1980	2,8,9,11,12,13,14,15	G,M
	22/ 5/1980	3,4,5,6,16,17,18	G,M
49	3/ 6/1980	3,4,6,16,17,18	G,M
	4/ 6/1980	2,5,8,9,11,12,13,14,15	G,M
50	18/ 6/1980	2,8,9,11,12,13,14,15	G,M
	19/ 6/1980	3,4,5,6,16,17,18	G,M

Table 2: continued.

Survey[1]	Dates	Reefs	Observers[2]
51	2/ 7/1980	3,4,5,6,16,17 18	G,M
	4/ 7/1980	2,8,9,11,12,13,14,15	G,M
52	16/ 7/1980	8,9,11,12,13,14,15	G,M
	17/ 7/1980	2,3,5,6,16,17,18	G,M
53	29/ 7/1980	3,4,5,6,16,17,18	G,M
	30/ 7/1980	2,8,9,11,12,13,14,15	G,M
54	11/ 8/1980	2,3,4,5,6,8,9 11,12,13,14,15,16,17,18	G,M

1: C = Construction time
2: G = D. Gascon; M = R. Miller

and small reefs started at survey no. 40, the intervening six weeks being used for dismantling, construction and subsequent modifications of the study site.

The encrusting fauna and flora were also qualitatively estimated and collections taken at irregular intervals to provide proper identification. Difficulties were encountered during summer censusing, when thick mats of macroalgae and hydroids covered the reefs, making fish counts difficult.

Tagging procedure

To assess length of residence by fish on artificial reefs, fish on reef no. 4 were tagged. Only one reef was used for the tagging experiment, because I was unsure of the effects of the procedure on the fish community. A fish was captured from the reef with a slurp gun and brought to the surface where four coloured embroidery beads were attached to the dorsal musculature with a nylon monofilament line, under MS222 anaesthetic. Great care was taken so that enough line was used to avoid unnecessary constriction of the flesh. As soon as the fish had recuperated, it was returned to its reef by the divers. The tagging procedure is the same as that employed by Craik (1978).

Removal experiments

In May 1980, two species of rockfish (*Sebastes caurinus* and *S. maliger*) were selectively removed by spearing from artificial reefs in order to detect competitive interactions between them. Two or three dives were required to complete a total removal of rockfish from one reef. Table 3 presents a detailed schedule of the removal work. Fish became extremely difficult to catch after a few attempts which explains the length of time required for complete removals. *Sebastes caurinus* were entirely removed from reef no. 5, *S. maliger* from reef no. 4, and both species from reef no 3. Reefs no. 2 and 6 were left as controls.

Rock rubble fish estimation

The main source of colonists to the artificial reefs was presumed to be the rock rubble area. The abundance and diversity of fish inhabiting the rock rubble slope was estimated by counting all the fish visible in two 50 x 2 m. strip transects (Keast and Harker, 1977). The fish counts on the transects were started in July 1978, and were continued until the end of the study, with the exception of the period

Table 3: Removal schedule.

Date	Reef
10/5/80	3,4
11/5/80	3,4,5
12/5/80	3,4
16/5/80	5

September–December 1979, when I was in Edmonton. The sampling intervals were one month until December 1978, when the frequency was increased to two per month thereafter so I could keep track of the short-term fluctuations.

The upper transect was located just below the kelp bed (Fig. 4) (water depth 2–3 m at mean low water), whereas the lower transect was located just above the rock–sand interface at the base of the rock rubble slope (5–6 m deep at MLW). A third strip transect (called the sand transect) was laid on the sandy area at the base of the slope.

The transects were delimited by ropes, and markers at every 5 metres subdivided them into contiguous quadrats. The sampling was conducted in a fashion similar to the reef censusing. R. Miller and I would each count all fish seen in one half (upper and lower 1 m width) of the transect. However, during the counts some of the markers were missed – usually because they were covered by algae or animals – thus making the number of contiguous 5 m^2 sections effectively smaller (17–19). As for the reefs, estimated length and position of each fish were recorded. Because we could not use the reefs as a reference for the length estimates, a small ruler was carried. The position were recorded into two categories: substratum (1: rock; 2: sand; 3: kelp; 4: other) and position (1: exposed, resting on top of a surface; 2: exposed, resting against a vertical surface; 3: in a hole; 4: swimming).

Eight 4 m^2 quadrats were poisoned with an ichthyocide (Chem Fish Collector, Blue Spruce International, New Jersey). These quadrats were located on a smaller patch of rubble on the West side of the island. They had been delimited with yellow

rope prior to the application of the poison. For various reasons (temperature, surge, currents), the ichthyocide never worked satisfactorily and the technique was subsequently abandoned. Nevertheless 56 fish were collected, providing some insight to the composition of the cryptic community.

III. RESULTS I:

The fish community of the rock rubble slope

With the exception of a few studies (Moulton, 1977; Leaman, 1980), very little information on the ecology of Northeast Pacific reef fish exists. In order to make meaningful interpretations of the artificial reef results, baseline data on the communities inhabiting reefs surrounding the experimental habitat was required. In this chapter I have reported the results of the observations made on the fish community inhabiting the rock rubble slope facing the reefs using underwater strip transects.

A. Results

Twenty-five species were seen on the rock rubble slope: 23 on the upper transect and 18 on the lower transect. Sixteen of these species were seen on both transects. (Table 4). Eight species accounted for 98.2% of the observed fish, the goby, *Coryphopterus nicholsi*, representing by itself 86.8% of the sightings. Five species were seen only once, and of the species that were seen on one transect only, none were recorded more than twice (2 schools of *Cymatogaster aggregata* and *Brachyistius frenatus*).

The poisoning of 32 m^2 of rock rubble produced specimens of 7 species, 5 of which belonged to the species dominant in the visual censuses (*C. nicholsi, H. decagrammus, S. caurinus, S. maliger, S. melanops*). The two others were the nocturnal *Nautichthys oculofasciatus* (Moulton, 1977) and the crevice-seeking *Xiphister mucosus*, which are nearly impossible to detect visually due to their secretive habits.

Very few fish were seen on the sand transect (Appendix II), the recorded densities ranging from 0 to 0.2 fish/m^2. Except for *Hexagrammos decagrammus*, the community on the sand was made of an entirely different set of species (eg. Chimaeridae, Pleuronectidae).

Seasonal fluctuations

The mean density of the fish on the transects fluctuated greatly with the time of the year (fig. 6). The peaks of abundance occurred in summer (July-August), whereas the lowest densities were found in late winter (March-April) (Fig. 6). The

Table 4: List and numbers of the species encountered on the rock rubble slope

Species	Rotenone quadrats	Upper Transect		Lower Transect	
		78-79	79-80	78-79	79-80
AULORHYNCHIDAE					
Aulorhynchus flavidus	–	–	98	–	1
EMBIOTOCIDAE					
Brachyistius frenatus	–	5	–	–	–
Cymatogaster aggregata	–	12	–	–	–
Rhacochilus vacca	–	2	–	–	–
STICHAEIDAE					
Anoplarchus spp.	–	1	1	–	–
Chirolophis spp.	–	1	–	1	1
Xiphister mucosus	3	–	–	–	–
PHOLIDAE					
Apodichthys flavidus	–	1	–	–	–
Pholis laeta	–	4	4	2	2
ANARHICHADIDAE					
Anarrhichthys ocellatus	–	–	7	4	6
GOBIIDAE					
Coryphopterus nicholsi	39	2189	1681	2377	3711
SCORPAENIDAE					
Sebastes auriculatus	–	–	1	–	–
Sebastes caurinus	2	40	33	12	3
Sebastes maliger	3	85	43	28	38
Sebastes melanops	7	88	156	7	38
Sebastes pinniger	–	4	65	3	256
HEXAGRAMMIDAE					
Hexagrammos decagrammus	1	83	78	60	32
Hexagrammos stelleri	–	–	1	–	–
Ophiodon elongatus	–	8	3	8	1
Oxylebius pictus	–	15	45	6	17
COTTIDAE					
Artedius spp.	–	3	12	11	5
Enophrys bison	–	–	–	–	1
Hemilepidotus hemilepidotus	–	2	–	1	–
Jordania zonope	–	12	9	8	32
Nauthichthys oculofasciatus	1	–	–	–	–

Table 4: continued.

Species	Rotenone quadrats	Upper Transect		Lower Transect	
		78-79	79-80	78-79	79-80
Rhamphocottus richardsoni	–	–	–	1	–
Synchirus gilli	–	–	10	–	1
TOTAL	66	2555	2248	2529	4152

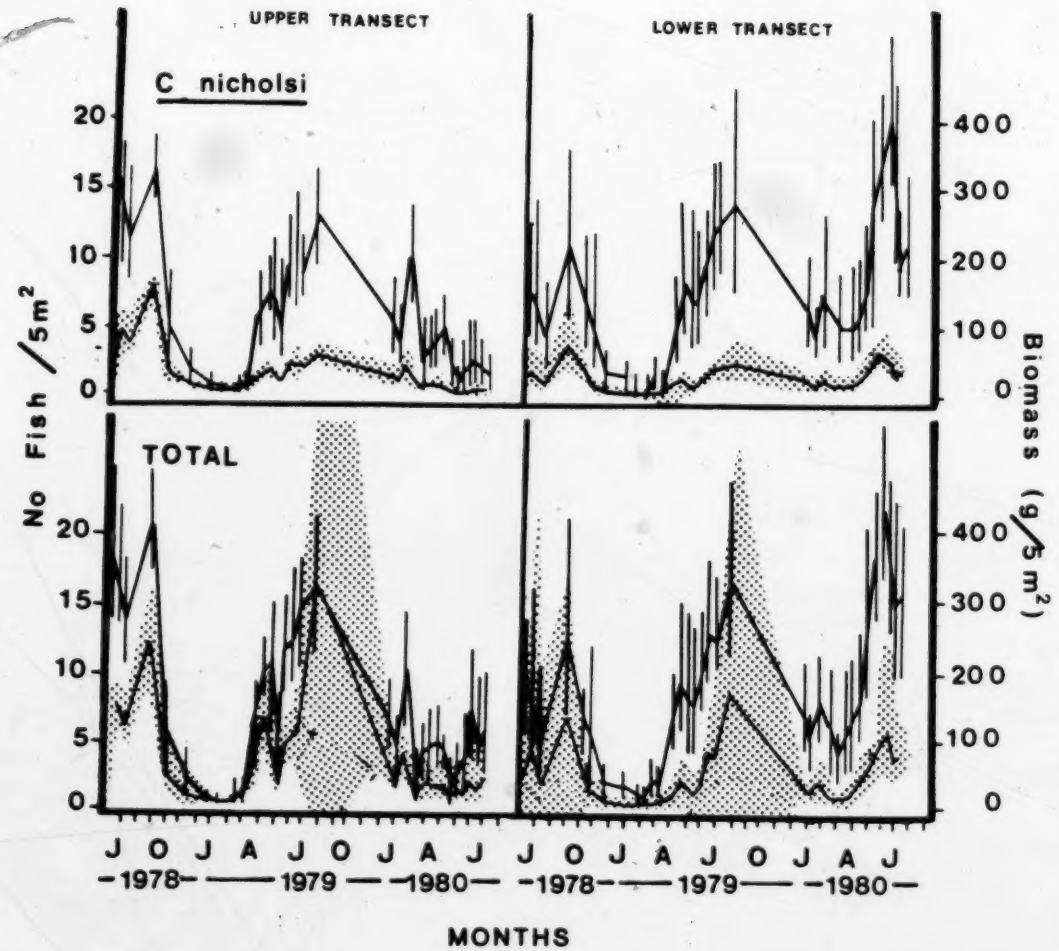

Figure 6: Seasonal fluctuations in the abundance and biomass of all species combined, and of *Coryphopterus nicholsi*, on the transects. The vertical bars indicate the 95% confidence limits and the grey shading indicates the 95% confidence belt around the mean biomass (fine lines)

densities estimated in biomass (from 5 g to 60 g/m² [50 to 600 kg/hectare]) show predictably the same patterns, although the variances are much larger. The biomasses were estimated from the length observations, using published length–weight relationships (Moulton, 1977), and one that was calculated on the *C. nicholsi* collected during the poisoning.

In addition to strong seasonal changes, large differences existed between years in both the high and low densities. The densities on the upper transect were highest at the beginning of the study and steadily declined thereafter, the peak density of 1980 being approximately 2.5 times smaller than in the first two years (Fig. 6). The opposite occurred on the lower transect. The decrease in density on the upper transect was apparently the result of the constant increase of the alga bed of *Desmarestia ligulata*, which created a totaly unsuitable habitat for the dominant *C. nicholsi* on the upper transect. The overall densities on the rock rubble slope (weighted means of the two transects) remained remarkably constant over the years (1978: 11.38; 1979: 15.95; 1980: 14.18 fish/5 m²), the decrease on the upper transect being compensated for by an increase on the lower transect.

The two winter lows were apparently different, the densities being approximately 10 times higher in 1980 than in 1979. The seasonal fluctuations in the abundance of each species followed closely the pattern described for the community as a whole (Fig. 6, 7). With the exception of *C. nicholsi*, all the species were encountered more frequently on the upper transect (Table 4).

Diversity

Species diversity on the transects was calculated using the Shannon–Weaver Index (Pielou, 1975), on both numbers and biomass estimates. Diversity as estimated by these two measures, and the number of species were all higher in the summer (Fig. 8). The estimates using biomass tended to be more variable (both on the short–term and the long–term) than those calculated for numbers alone. Species diversity was low, ranging from $H' \approx 0.3$ in the winter to $H' > 1.0$ in the summer, a consequence of the extreme dominance of *C. nicholsi*. The range of biomass diversities was greater ($0.1 < H' < 2.0$).

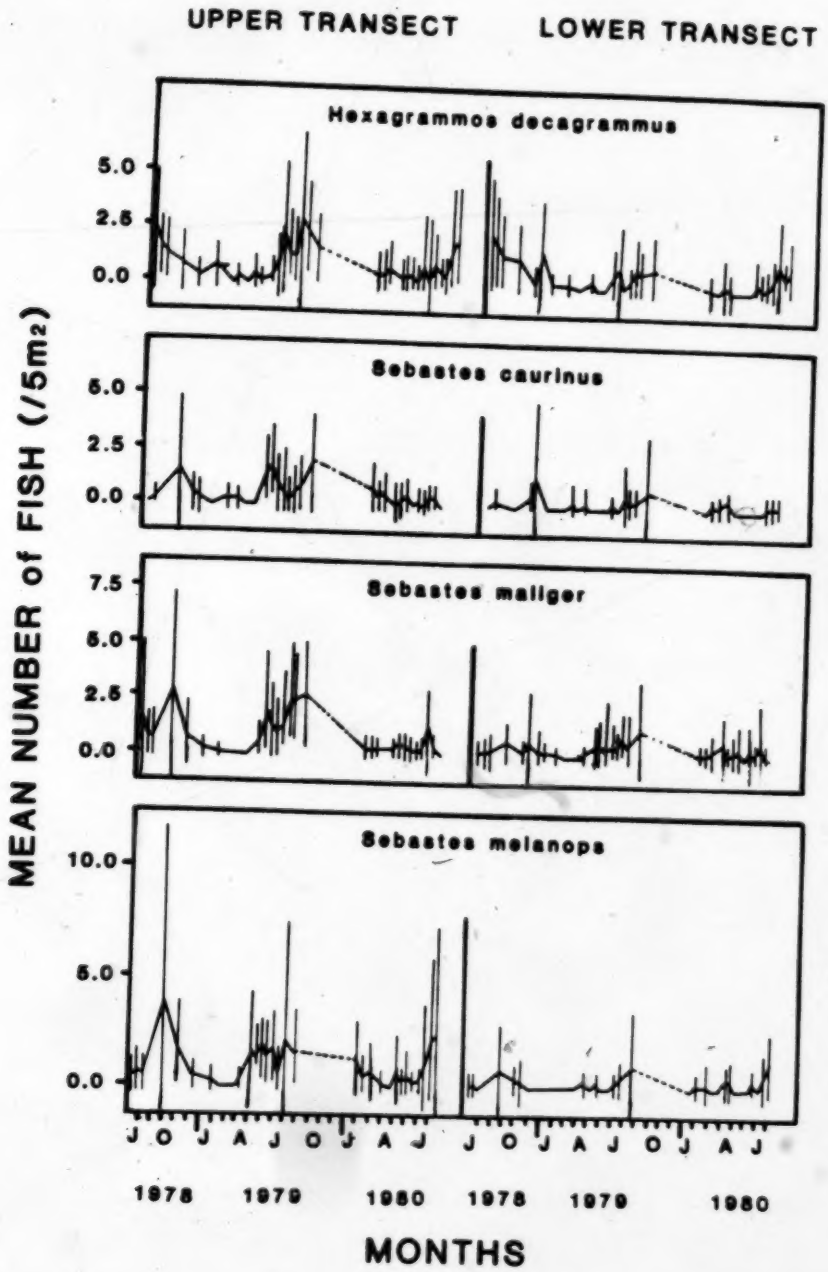

Figure 7: Seasonal fluctuations in the abundance of *Sebastes caurinus, S. maliger, S. melanops* and *Hexagrammos decagrammus* on the transects The vertical bars indicate the 95% confidence limits A 4 month gap in sampling (Sept. 1979–Jan. 1980) is indicated with dashed lines.

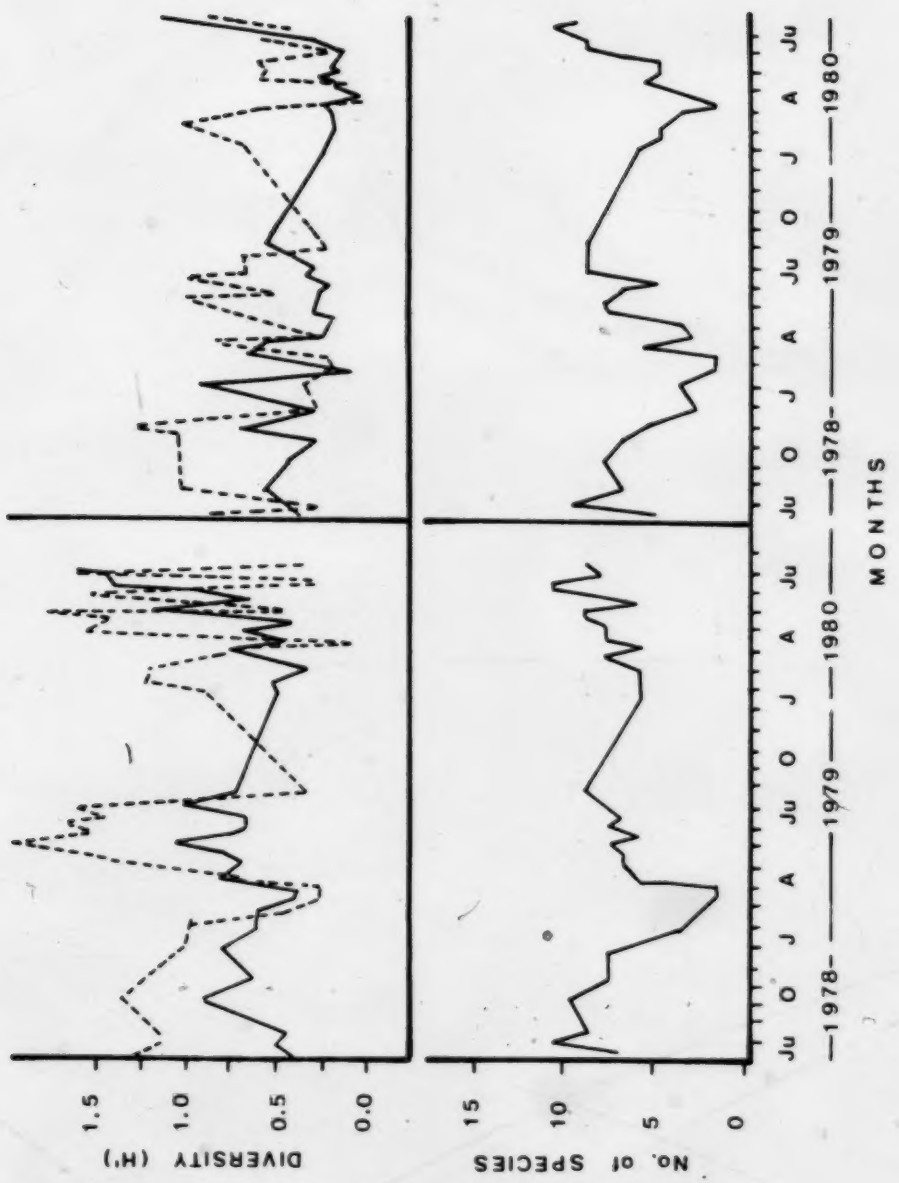

Figure 8: Seasonal fluctuations in the number of species and in species diversity on the transects Above, diversity: Solid lines are the estimates based on numbers; dashed lines are the biomass estimates. Below: number of species. Left: upper transect; right: lower transect

Space use

The pattern of space use by the five common species changed over the year (X^2, $P<0.01$ in all cases) (Fig. 9). The deletion of the somewhat unreliable estimates of fish under cover does not alter this conclusion. The observations on space utilization were grouped in 3-month periods for the purpose of the analysis.

Only *C. nicholsi* and *H. decagrammus* were regularly encountered over the sand, whereas the rockfish were almost exclusively restricted to rocky substrates. The rockfish tended to be found under cover more frequently than *C. nicholsi* or *H. decagrammus*, and all species were found under cover more frequently in winter than in summer (Appendix IV).

B. Discussion

Underwater transects have been used extensively in recent years (eg. Alevizon and Brooks, 1975; Brock, 1954; Chave and Eckert, 1974; Ebeling *et al.*, 1980; Keast and Harker, 1977) as a means of estimating the non-cryptic component of demersal fish communities. Most transects used covered larger areas than in the present study (3 to 19 times), the investigators concentrating on the larger species. Because of their sheer numbers, the smaller species are inadequately sampled or overlooked by divers swimming rapidly over great distances. The shorter transects used here allowed us to concentrate on the smaller species (Gobiidae, Cottidae, juvenile *Sebastes spp*). As a result the larger species (Hexagrammidae, adult *Sebastes spp*) were inadequately sampled; the small area covered by the subsections of the transects (5 m^2), was small in relation to the home range of these fish, creating a large degree of within transect variance for these species. The high variability in biomass and biomass estimates of diversity is a direct result of this: small variations in the number of these large, and consequently infrequent species, created large fluctuations in biomass.

Visual censuses may severely underestimate the cryptic component of the fish community. Leaman (1980) used an ichthyocide to estimate fish populations quantitatively in the kelp beds of Barkley Sound; he found large numbers of cryptic Cottidae, Stichaeidae and Liparidae in his samples. The poisoning done on the rock

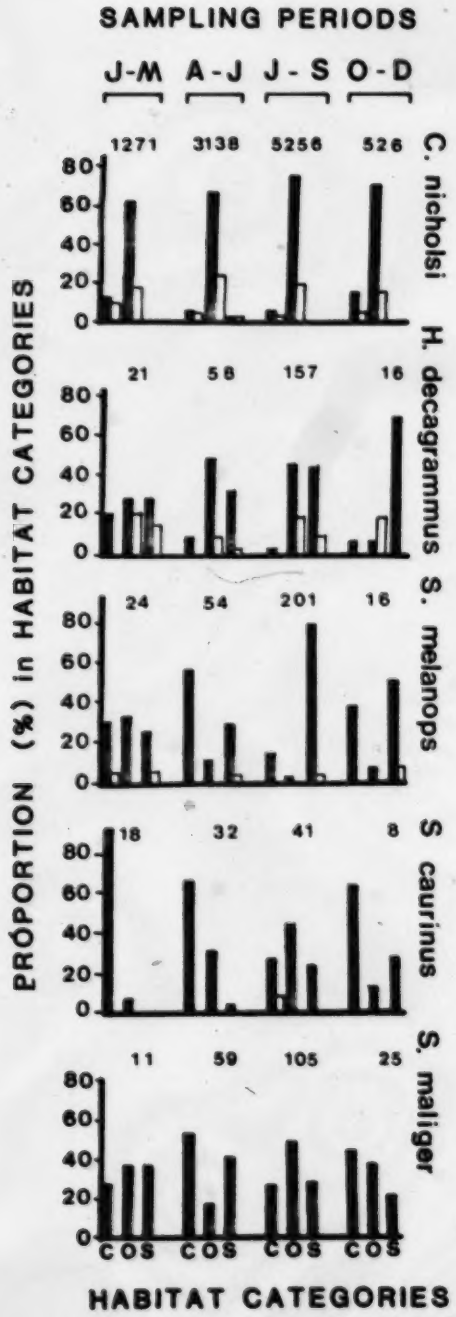

Figure 9: Seasonal changes in microhabitat use by the 5 commonest species on the transects White bars: sand; Black bars: rocks. Categories abbreviations: C: under cover; O: open; S: swimming.

rubble indicated that the cryptic component was relatively unimportant in the habitat of this study, as 90% of the fish collected belonged to the dominant species of the visual samples (the 7 species collected formed 93.9% of the sightings).

The most noticeable aspect of this community was the large seasonal fluctuations in densities (of up to 10 times). Such fluctuations have been reported for other temperate nearshore communities, especially those of soft bottom habitats (Adams, 1976; Allen and Horn, 1975; Modde and Ross, 1980), although deeper temperate reefs may be more seasonally stable (Ebeling *et al*. Stephens and Zerba, 1981). Contrary to soft bottom species, rocky reef fish species are usually quite sedentary (Chapter IV, Leaman, 1980; Love, 1979; K.S. Cole, personal communication). The seasonal differences result probably from the fish seeking cover more frequently at low temperature, rather than emigration, as from shallow sandy habitats (Modde and Ross, 1980). All species were observed more frequently under cover in winter, giving some weight to this hypothesis. Most of the fish under cover were probably overlooked, as they are extremely difficult to see, but the increase in relative abundance of fish seeking cover indicates that many more fish may have been present.

The biomass estimates are average and agree favourably with other published estimates (see Moulton, 1977 for a review). The biomass fluctuated from 50 kg/ha in winter to 600 kg/ha in summer, the latter estimate being probably closer to the actual standing crop, as most of the fish were visible and counted. My estimate is somewhat higher than other temperate estimates (Moulton, 1977: 169–311 kg/ha; Quast, 1968b: 300–380kg/ha), but because of the very large variances associated with these estimates, the differences between them are certainly not significant.

The extreme dominance (in terms of abundance) of one species, *C. nicholsi*, and the ensuing low diversity (H'=0.2–1.0) are reminiscent of soft bottom communities. The habitat selected for the study was extremely homogeneous and the shortness of the transects allowed me to keep habitat variation to a minimum, providing only the alpha – within-habitat – component of diversity (Pielou, 1975); hence the similarity to soft bottom environments where habitats are also uniform and simple. Allen and Horn (1975) reported values of H'=0.1–1.0 for a California lagoon and Adams (1976) gave

values of H'=0.4–1.8 from eel grass beds of North Carolina. On the contrary, typical reef habitats are more varied, enhancing the between-habitat (beta diversity) component; Ebeling *et al.* (1980) reported values of H'=1.4–2.8 for southern California reefs.

The community was remarkably stable over the years, in terms of both the species present and of their absolute abundance. The overall density of *C. nicholsi* remained constant between 1978 and 1980, although its depth distribution changed. The continual increase of the size of the bed of *Demerestia ligulata* (of unknown causes) appear to have forced the *C. nicholsi* inhabiting the upper reaches of the habitat to retreat to deeper water since it is almost never encountered in kelp beds (Leaman, 1980). The local increase in density (3 to 5 times) at the base of slope indicates that, at least at the low densities of 1980, the population of *C. nicholsi* was probably below the carrying capacity of the environment. In winter, the cover of *Demerestia* was absent, and it cannot be responsible for the differences between years. The minimum temperature registered in 1979 was 2.5°C lower than in 1980 (6.5° *vs* 9°), which may have provoked the fish to seek cover more frequently in 1979. Ebeling *et al.* (1980) found that the demersal component of kelp-bed fish assemblages was relatively constant from year to year, whereas the abundance of many species fluctuated greatly on a southern California reef (Stephens and Zerba, 1981).

Measure of stability in fish community is highly scale dependent (Anderson *et al.*, 1981), and there is no way to determine *a priori* the appropriate scale. For example, many of the variable species described by Stephens and Zerba (1981) are schooling roamers, and the scale used in their study may have been too small, in relation to their home range to estimate their abundance accurately. The results indicate that a 100 m^2 area was adequate to follow the dynamics of a small (5–12 cm) demersal species, but that it was not for the larger ones, creating a large degree of variability.

IV. RESULTS II:

The colonization history of the reefs

In spite of their frequent use in the study of reef fish communities (Russell *et al.*, 1974; Molles, 1978; Talbot *et al.*, 1978; Bohnsack and Talbot, 1980), the appropriateness of artificial reefs (i.e. how well they sample natural communities) has never been examined in detail. Furthermore, autecological information on the species present is usually lacking, the biological information usually being limited to species lists and counts.

However, in order to make meaningful attempts to develop hypothesis on the working of these communities, one has to have a solid data base on the life history of the species present. In this chapter, I will examine two points:

1. The appropriateness of these reefs as a sampling tool for the rock rubble fish community, by comparing the community composition and density in both systems.
2. The patterns of community development and composition on the three initial series of reef (winter and summer insulars, continentals), concentrating on the patterns of colonization, recruitment, abundance and distributions of the commonest species.

I will also examine the effects of isolation on community structure. Artificial reefs are usually built in isolation – in order to produce independent systems – but the effects of varying dispersal abilities among the species have never been looked at. The continental reefs were constructed to estimate this effect, and the differences between the insular and continental reefs should provide an estimate of the dispersing abilities of the species.

Finally, contrary to what happens in tropical waters where recruitment is largely aseasonal, species of fish inhabiting Barkley Sound have well delimited reproductive periods (Hart, 1973). Using the two series of insular reef (summer and winter), I also examine the hypothesis that this strong seasonality will affect community development, in a similar way to that reported by Sutherland (1974, 1981) for fouling communities.

A. Results

Invertebrates and algae rapidly colonized the artificial reefs. Thick growths of hydroids (*Obelia spp.*), serpulid worms and encrusting coralline algae developed in a few months. Large seaweeds (mainly *Nereocystis luetkeana, Costaria costata, Laminaria spp., Ulva spp.,* and *Porphyra spp.*) grew rapidly in spring and early summer. These algae were usually eliminated by sea urchins (*Strongylocentrotus franciscanus*) although in some instances they were allowed to persist late in the season, reaching considerable size. The growth of all encrusting organisms reached its maximum in late summer. The list of invertebrates and algae collected from the reefs is given in Appendix I.

Thirty-five species of fish, belonging to 14 families, were recorded from the artificial reefs (Table 5). The species were categorized as residents or transients (Talbot *et al.*, 1978), based on knowledge of their general habitat requirements (see literature review section of the Introduction) and on whether they usually remained in the immmediate vicinity of the reefs, or fled when disturbed by the divers. Twenty-seven species were categorized as residents (including all the common species). Almost all the species found on the the reefs were seen on the two rock transects, with the exception of a few rare ones. The species present on the sand transect were seen only rarely on the reefs; thus the reefs were attracting a community typical of rocky environments. Schooling individuals of *Sebastes melanops* were not included in the analysis due to their weak association with the reefs, and because of the great difficulty of accurately estimating their numbers.

Resident species comprised 82.7% of the individuals sighted (99.2%, when the estimates for the schools of *S. melanops* are omitted). Eight species comprised over 96% of the residents. These 8 species can be easily divided into 2 categories: 4 species of rockfish (*Sebastes caurinus, S. maliger* (Plate II.3, Plate II.4), *S. melanops* and *S. pinniger*), and 4 benthic species (*Coryphopterus nicholsi* [Plate II.1], *Hexagrammos decagrammus* [Plate II.2], *Jordania zonope*, and *Artedius spp.*). This latter "species" probably includes *A. harringtoni, A. fenestralis* and *A. lateralis*, which were all collected from the study site in preliminary samplings; they are virtually impossible to recognise under water and no attempts were made to separate them. They are counted as one species throughout the thesis.

Table 5. List and total abundance of the species encountered on the reefs. Nomenclature follows Hart (1973)

Species	Age[1]	Status[2]	Number on[1]				
			W.I.	S.I.	N.I.	S.R	C.R
BATRACHOIDIDAE							
Porichthys notatus (Plainfin midshipman)	a	t	1	–	–	–	–
GOBIESOCIDAE							
Gobiesox meandricus (Northern clingfish)	b	r	3	–	–	–	2
GADIDAE							
Merluccius productus (Pacific hake)	j	t	1	–	–	–	–
AULORHYNCHIDAE[4]							
Aulorhynchus flavidus (Tube-snout)	b	t	–	–	–	–	5
EMBIOTOCIDAE							
Brachyistius frenatus (Kelp perch)	j	t	4	9	–	–	3
Rhacochilus vacca (Pile perch)	j	t	16	–	–	–	3
PHOLIDAE							
Pholis laeta (Crescent gunnel)	b	r	2	2	–	–	–

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Table 5. continued.

Species	Age[1]	Status[2]	Number on[3]				
			W.I.	S.I.	N.I.	S.R.	C.R.
Pholis ornata (Saddleback gunnel)	b	r	4	–	–	–	1
Pholis sp.[5] (Gunnel sp.)	b	r	14	1	–	1	–
STICHAEIDAE							
Anoplarchus spp. (Cockscomb spp.)	b	r	1	2	–	1	1
Chirolophis spp. (Warbonnet spp.)	b	r	–	–	–	3	1
Xiphister mucosus (Rock prickleback)	b	r	1	–	–	–	–
Stichaeidae spp. (Prickleback spp.)	?	r	1	1	–	–	–
ANARHICHADIDAE							
Anarrhichthys ocellatus (Wolf-eel)	j	r	32	9	–	2	8
GOBIIDAE							
Coryphopterus nicholsi (Blackeye goby)	b	r	1429	592	94	229	1628

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Table 5. continued.

Species	Age[1]	Status[2]	Number on[3] W.I.	S.I.	N.I.	S.R.	C.R.
SCORPAENIDAE							
Sebastes auriculatus (Brown rockfish)	j	r	10	13	2	8	–
Sebastes caurinus (Copper rockfish)	b	r	304	178	10	11	159
Sebastes maliger (Quillback rockfish)	j	r	526	253	4	13	113
Sebastes melanops[6] (Black rockfish)	j (j)	r (?)	1639 (1145)	211 (43)	283 (235)	1 (–)	696 (288)
Sebastes mystinus (Blue rockfish)	j	r	1	–	–	–	7
Sebastes pinniger (Canary rockfish)	j	r	130	9	6	2	128
Sebastes spp. (Rockfish spp.)	j	r	58	40	4	4	66
HEXAGRAMMIDAE							
Hexagrammos decagrammus (Kelp greenling)	b	r	211	90	9	19	131
Ophiodon elongatus (Lingcod)	b	r	4	–	5	–	4

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Table 5, continued

Species	Age[1]	Status[2]	Number on[3] W.I	S.I.	N.I.	S.R.	C.R.
Oxylebius pictus (Painted greenling)	b	r	7	–	–	–	11
COTTIDAE							
Artedius spp.[7] (*Artedius* sculpins)	b	r	86	55	10	26	6
Artedius lateralis (Smoothhead sculpin)	b	r	1	1	–	–	1
Enophrys bison (Buffalo sculpin)	a	r	–	–	2	–	–
Hemilepidotus hemilepidotus (Red Irish lord)	b	r	2	3	–	–	1
Jordania zonope (Longfin sculpin)	b	r	138	37	38	45	168
Nautichthys oculofasciatus (Sailfin sculpin)	b	r	3	–	–	–	–
Rhamphocottus richardsoni (Grunt sculpin)	b	r	9	12	–	5	5
Scorpaenichthys marmoratus (Cabezon)	j	r	–	2	–	–	–
Unidentified cottid genus[8]	b	r	35	14	1	4	5

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Table 5, continued:

Species	Age[1]	Status[2]	Number on[3] W.I.	S.I.	N.I.	S.R.	C.R.
Cottidae spp. (Misidentified cottids)	b	r	22	10	3	8	7
AGONIDAE							
Agonopsis vulsa[9] (Northern spearnose poacher)	a	t	–	–	–	1	–
PLEURONECTIDAE							
Lepidopsetta bilineata (Rock sole)	b	t	16	2	–	1	3
Pleuronichthys coenosus (C-O sole)	a	t	1	–	–	–	–

NOTES

1. a = adults; j = juveniles; b = both
2. t = transients; r = residents
3. W.I. = winter insular reefs; S.I. = summer insular reefs; N.I. = new insular reefs; S.R. = small reefs; C.R. = continental reefs.
4. = Gasterosteidae (Robins *et al.*, 1980).
5. Probably *Pholis schultzi*, (red gunnel).
6. The numbers in parenthesis underneath indicate the number of *S. melanops* that were seen schooling above the reefs (considered as transient).
7. Includes *Artedius harringtoni* (scalyhead sculpin) and *A. fenestralis* (padded sculpin).
8. Possibly the intertidal genus *Clinocottus*.
9. = *Agonopsis emmelane* (Robins *et al.*, 1980).

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Plate II: Common species of fish present on the artificial reefs.
1: *Coryphopterus nicholsi*, approximately 8 cm long.
2: *Hexagrammos decagrammus* male, approximately 20 cm long.
3: *Sebastes caurinus*, approximately 12 cm long.
4: *Sebastes maliger*, approximately 10 cm long.

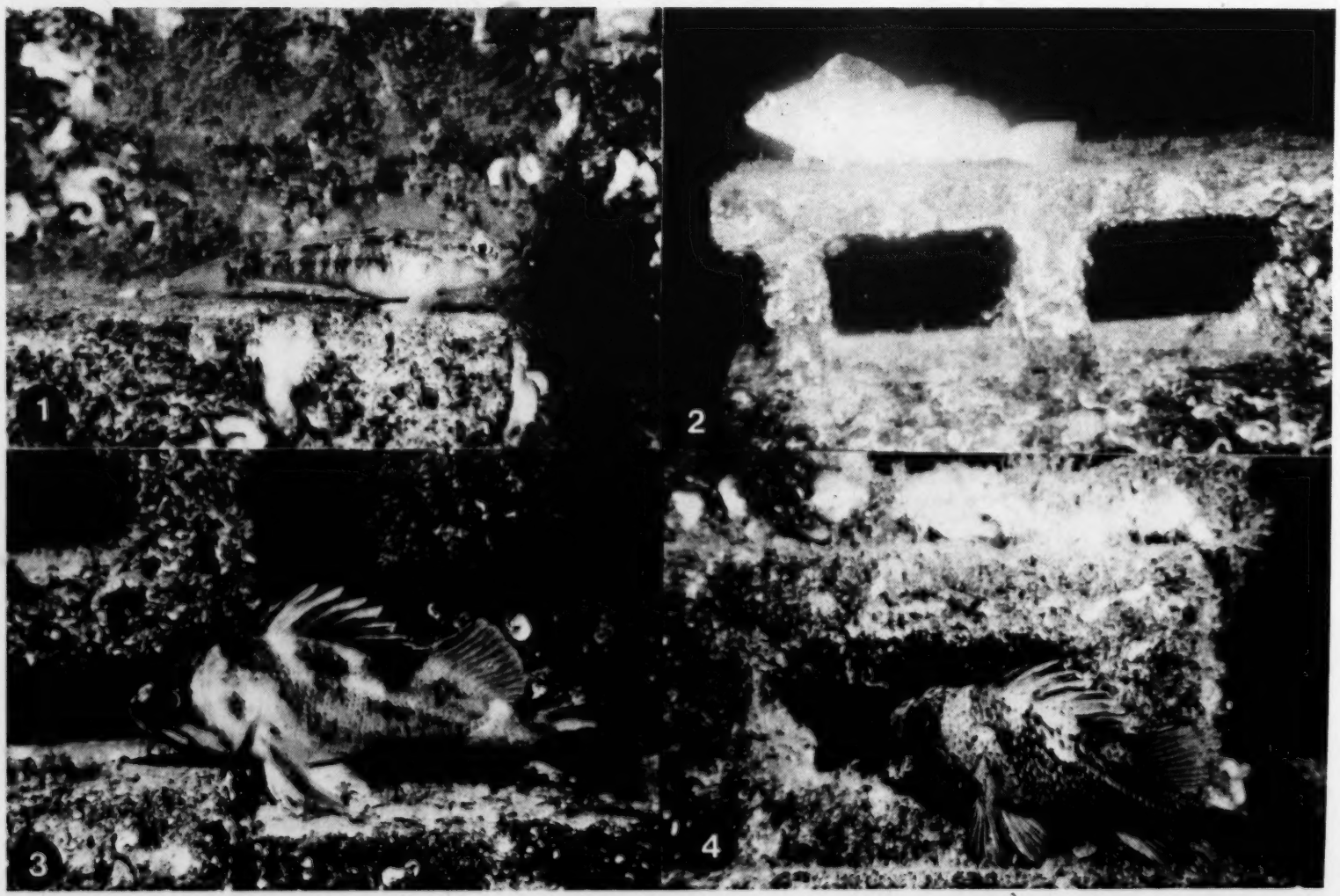
1
2
3
4

Figure 10 gives the order of appearance and the combined occupation periods by the species on the three main series of reefs.

Colonization of the artificial reefs

The colonization process was fastest for the continental reefs and slowest for the insular reefs. The mean number of resident species leveled within a few months at approximately 5 species/reef on all three series (Fig. 11). On this figure, as on all subsequent colonization curves, the two series of insular reefs are combined after a year, since no differences in their communities could be detected (see the last part of this chapter). To judge when the asymptotic number of species was reached, I used the following arbitrary criterion: four consecutive censuses with a mean number of species/reef $\geq$ 5. By this criterion, the asymptotic number was already reached on the continental reefs at the first census (Fig. 12), less than two weeks after construction. The winter insular reefs took 13 weeks, whereas the summer insular reefs took 24 weeks to reach the same level. The number of species did not show any seasonal trends, and it remained remarkably constant throughout the study.

Colonization in terms of number of individuals (resident species) followed a similar pattern, the continental reefs being filled almost immediately, whereas the insular reefs took several months. However, the mean number of fish/reef showed strong seasonal fluctuations (Fig. 12). The mean number of fish/reef during the summer peak (August–September) was approximately twice the numbers seen in the winter low (March–April) (25–32 fish/reef *vs.* 12–15 fish/reef).

The rates of colonization can be estimated from the colonization record. Immigration (i.e. the no. species at time $t + 1$ that were not present at time t, divided by the censusing interval in days) and emigration (= extinction [MacArthur and Wilson, 1967], i.e. the no. of species absent at time $t + 1$ which were present at time t, divided by the censusing interval in days) are plotted in Figure 13. Turnover rates (immigration and emigration) can be similarly calculated for individual fish (Fig. 14). All these rates exhibit a large degree of short term variability; furthermore there are indications of seasonal fluctuations in the turnover rates of species, immigration and emigration occurring faster in summer. If such trends existed for individual rates, they were entirely masked by the short term variability.

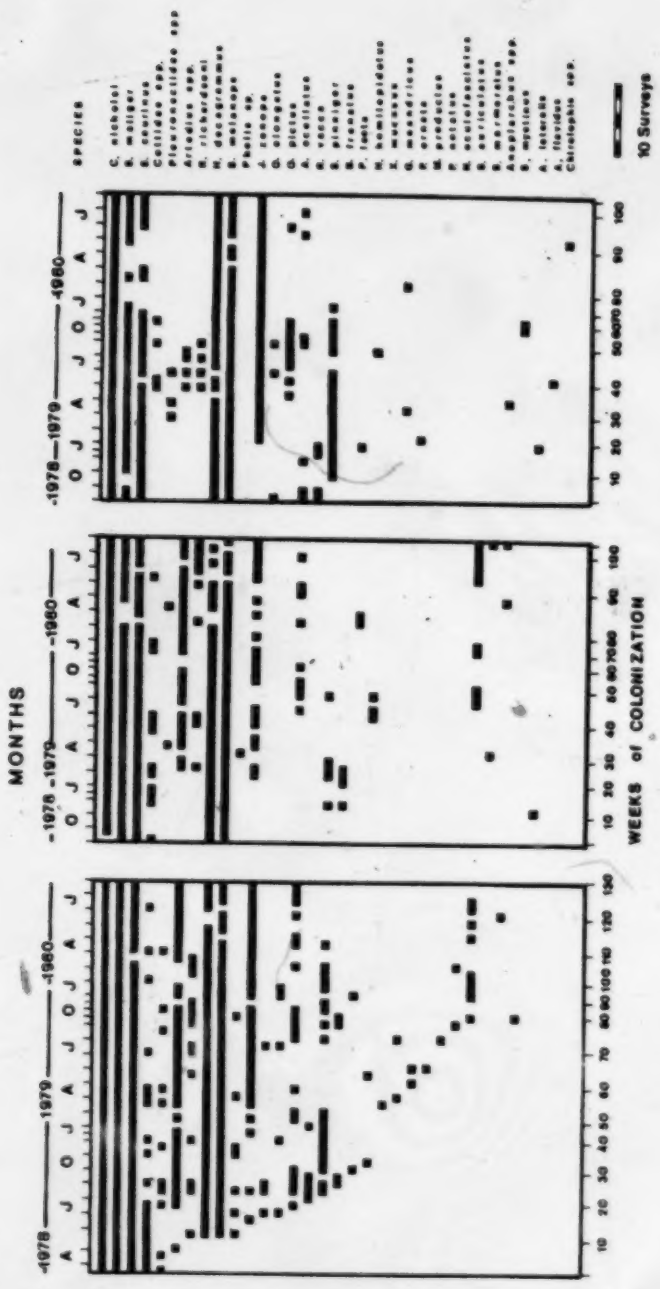

Figure 10: Detailed colonization history of the reefs. The black bars indicate when a species was present on reefs in each series. One black square equals one census period. Since the intervals between censuses were not all equal, the scale on the abcissa is not regular. Left: winter insular reefs; centre: summer insular reefs; right: continental reefs.

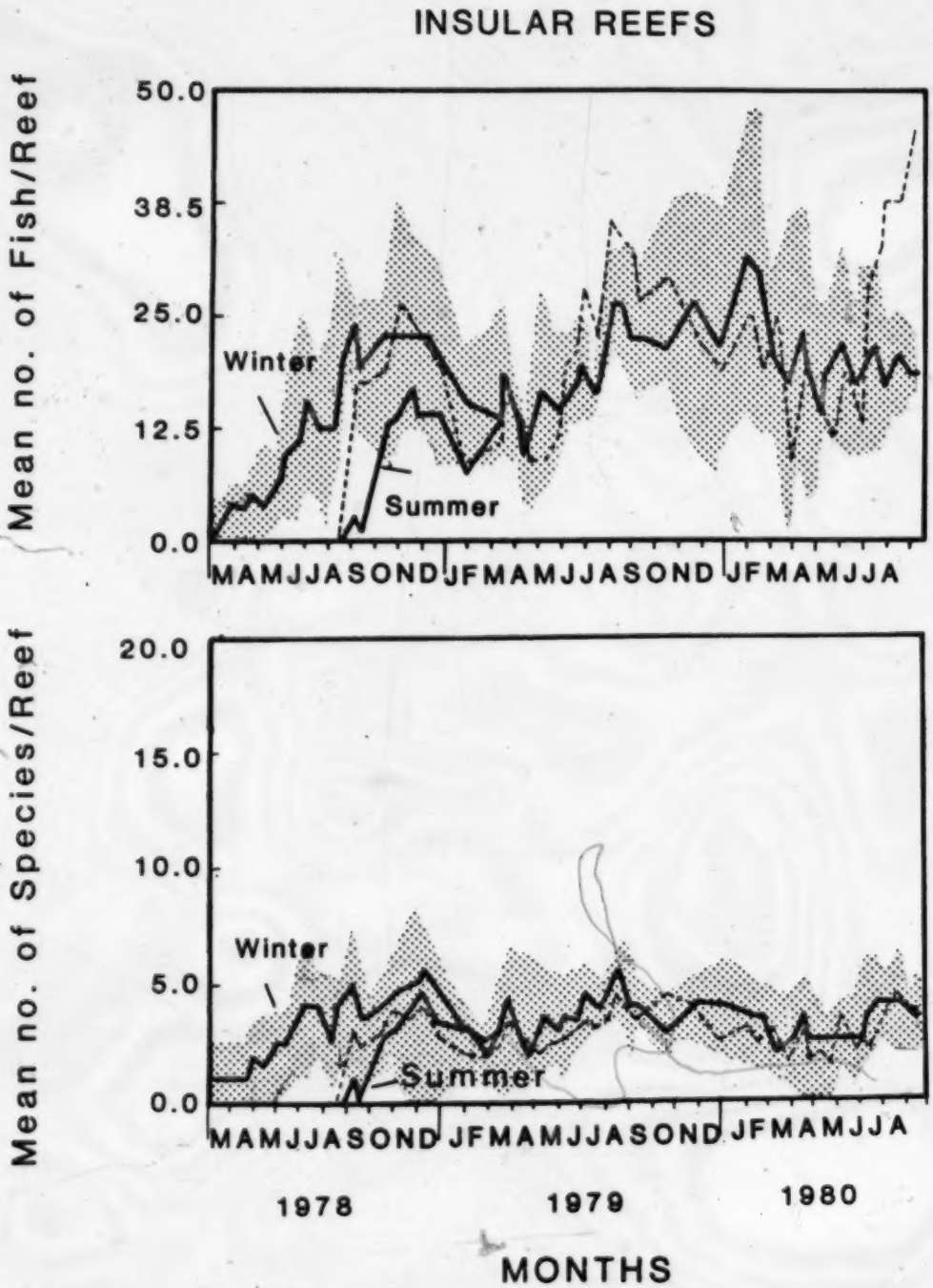

Figure 11: Colonization curves (species and number of fish) for the insular reefs. The shading represent the 95% confidence interval. The two series (winter=winter insular and summer=summer insular) are kept separate for the pre-equilibrium phase of colonization (6 months) but they are pooled together after that, as the 2 series became similar. The curve for the continental reefs (dashes) is given for comparison.

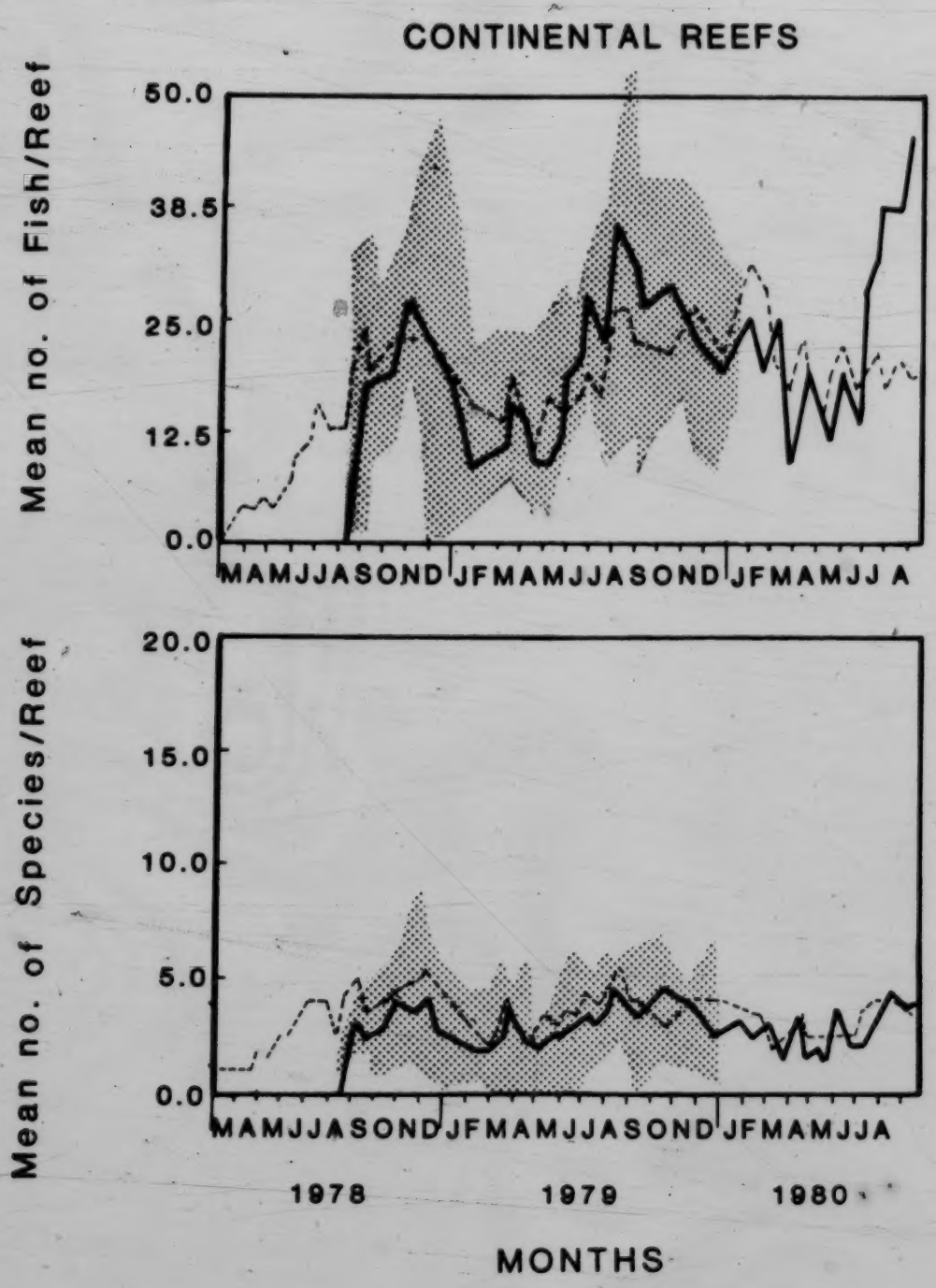

Figure 12: Colonization curves (species and number of fish) for the continental reefs. The shading represent the 95% confidence interval. The curve for the insular reefs (dashes) is given for comparison.

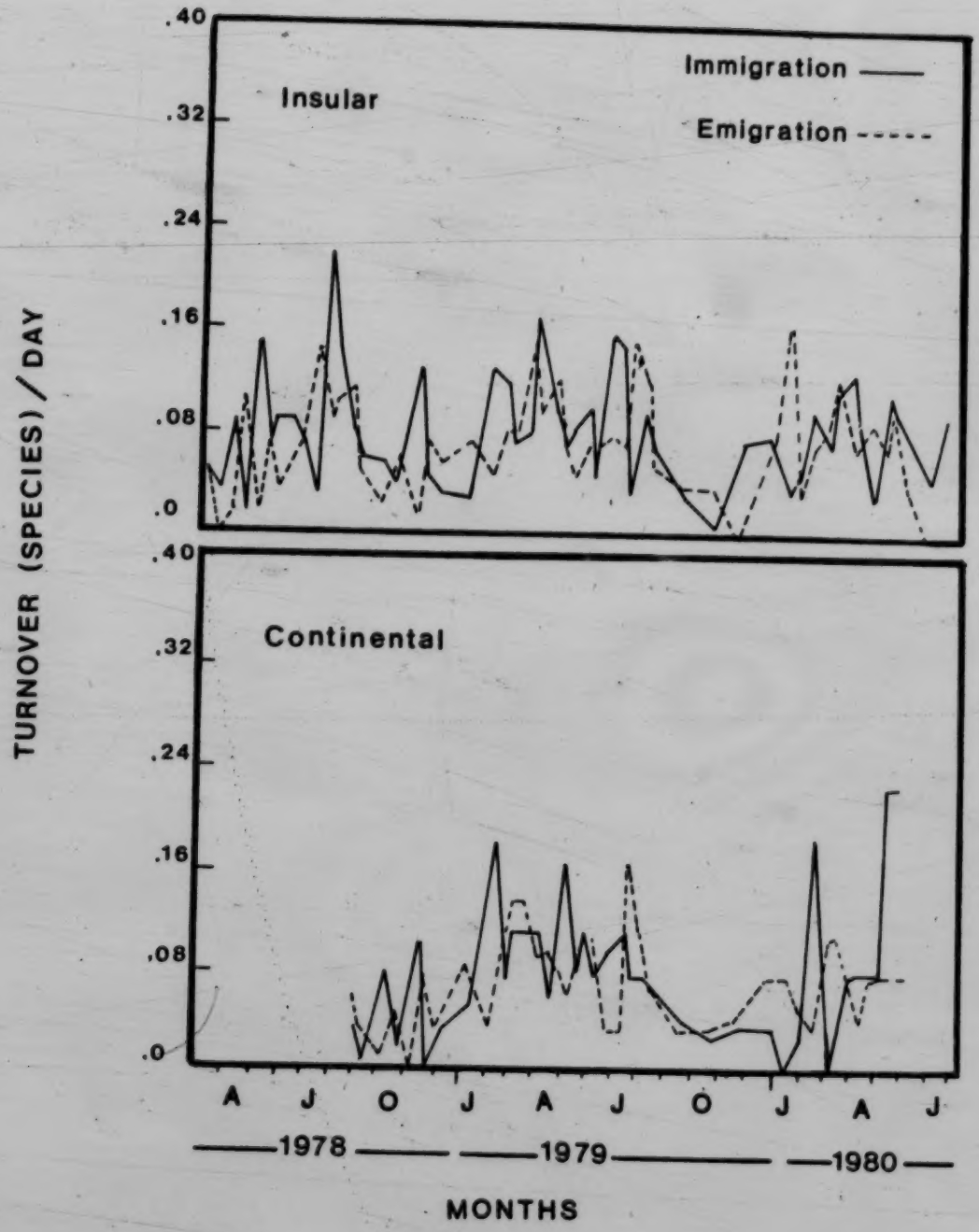

Figure 13: Species turnover on the insular and continental reefs.

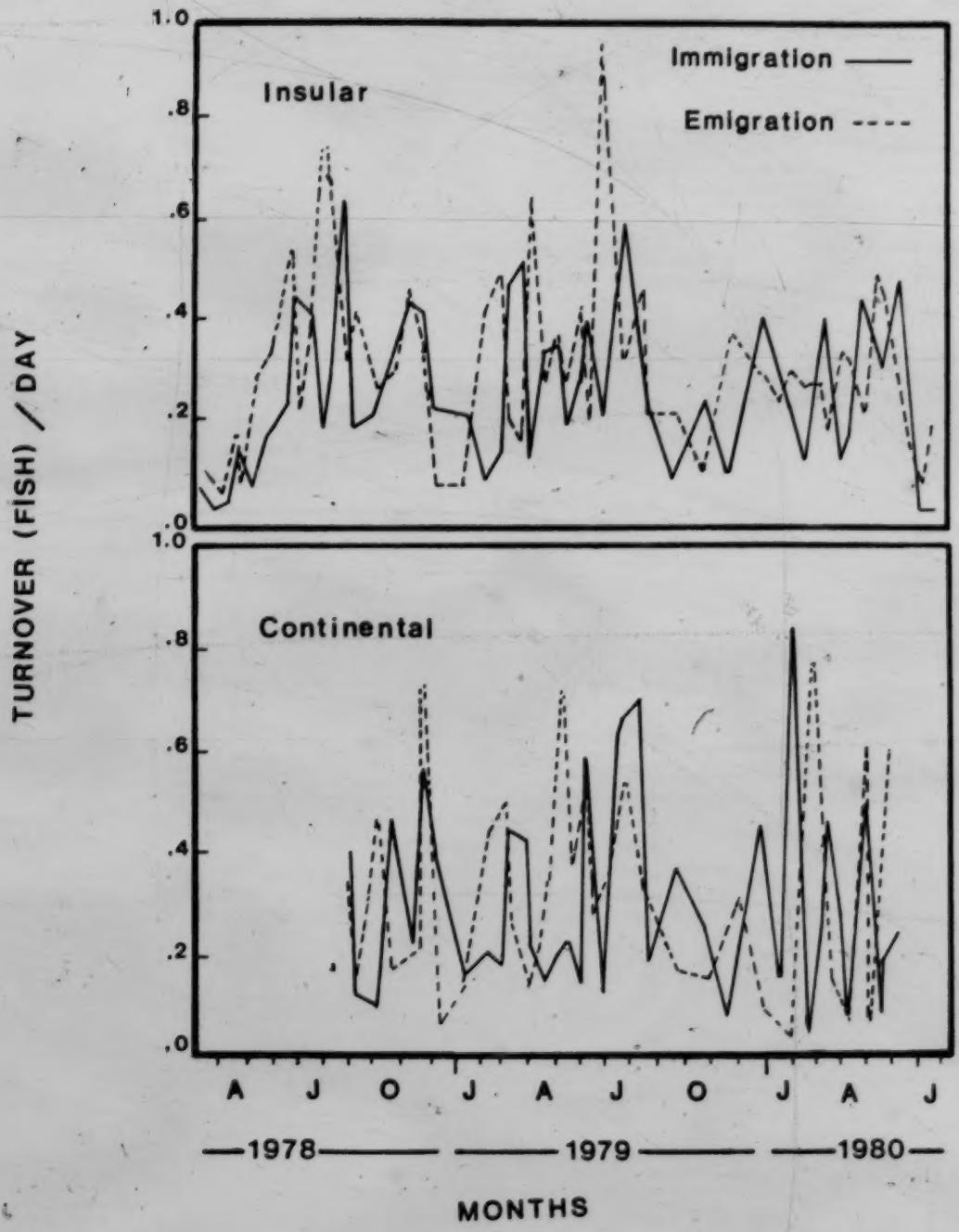

Figure 14: Turnover in the number of fish on the insular and continental reefs.

Initial colonization phase

When compared to the communities present at equilibrium, the community composition during the active colonization phase was unremarkable, the main difference being the number of fish.

On the winter insular reefs, representatives of the three dominant species (*C. nicholsi, S. caurinus, S. maliger*) had all appeared by the third census (one month), their order of appearance varying somewhat among the replicates (Appendix III). The other common species (*S. melanops, S. pinniger, H. decagrammus*) appeared later, but their appearance was closely tied to the arrival of young of the year of these species on the study site (see next section). On the summer insular reefs, the pattern was essentially similar, although members of the latter three species colonized the reefs as fast as the other species. The summer insular reefs were built after the recruitment period of *S. melanops, S. pinniger,* and *Hexagrammos decagrammus,* and these species were thus available for immediate colonization.

No evidence of succession (i.e. replacement of early arriving species by later arriving ones) could be detected in the early colonization record with possibly one exception. Sculpins (*Artedius spp.* or *Clinocottus spp.* – their identification in the early stages of the study might have been erroneous) were quite common on reef nos. 2 and 3, in the first few weeks, but they virtually disappeared thereafter. They did not reappear for several months (may be a different species?). However, these sculpins were never noticed in abundance at the beginning of the colonization of the three other series of insular reefs.

Only one of the eight common species (*J. zonope*) was virtually absent in the early history of the reefs, not being really common until 18 months after construction. This may be due either to biological facilitation (i.e. development of an appropriate encrusting biota) or to its general increase in abundance on the study site in 1979–1980 (see section on yearly differences).

Colonization history of individual species

The eight common species showed specific patterns of colonization and abundance (Fig. 15–22). Only *Sebastes melanops* and *S. pinniger* showed any seasonal fluctuations in abundance (Fig. 17, and Fig. 20). This fluctuation is caused by the

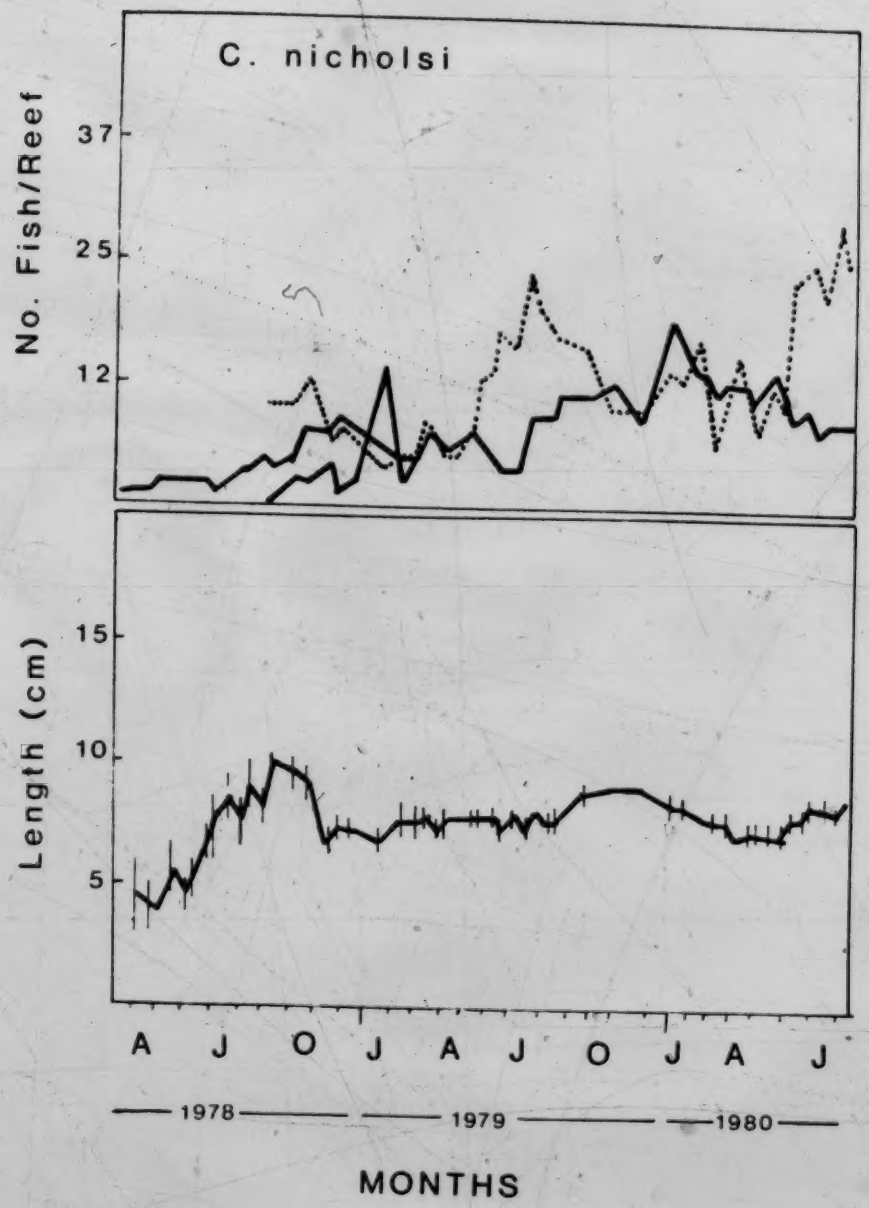

Figure 15: Seasonal changes in the abundance of *Coryphopterus nicholsi* on the artificial reefs. As in Figure 11, the 2 series of insular reefs are pooled. Solid lines: insular reefs; dashed line: continental reefs. The vertical bars around the mean lengths are the 95% confidence limits.

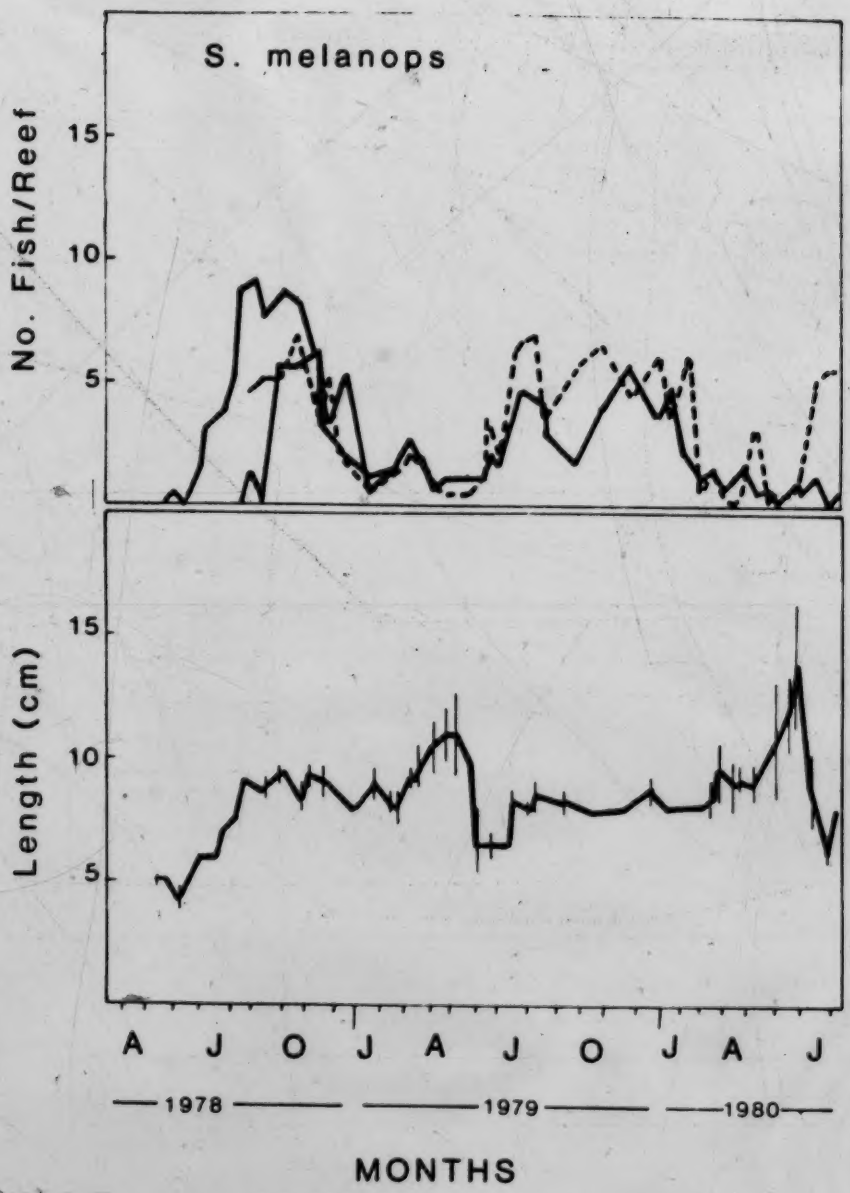

Figure 16: Seasonal changes in the abundance of *Sebastes melanops* on the artificial reefs. As in Figure 11, the 2 series of insular reefs are pooled. Solid lines: insular reefs; dashed line: continental reefs. The vertical bars around the mean lengths are the 95% confidence limits.

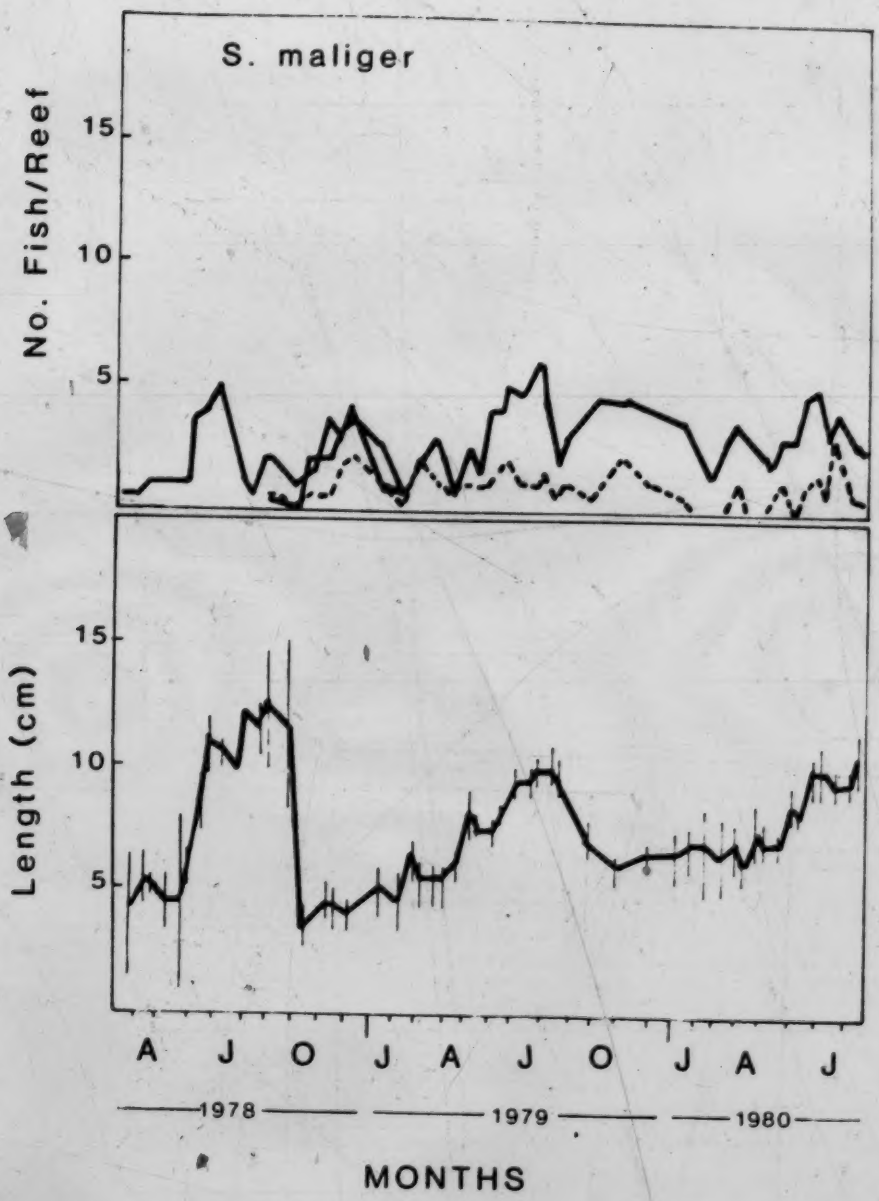

Figure 17: Seasonal changes in the abundance of *Sebastes maliger* on the artificial reefs. As in Figure 11, the 2 series of insular reefs are pooled. Solid lines: insular reefs; dashed line: continental reefs. The vertical bars around the mean lengths are the 95% confidence limits.

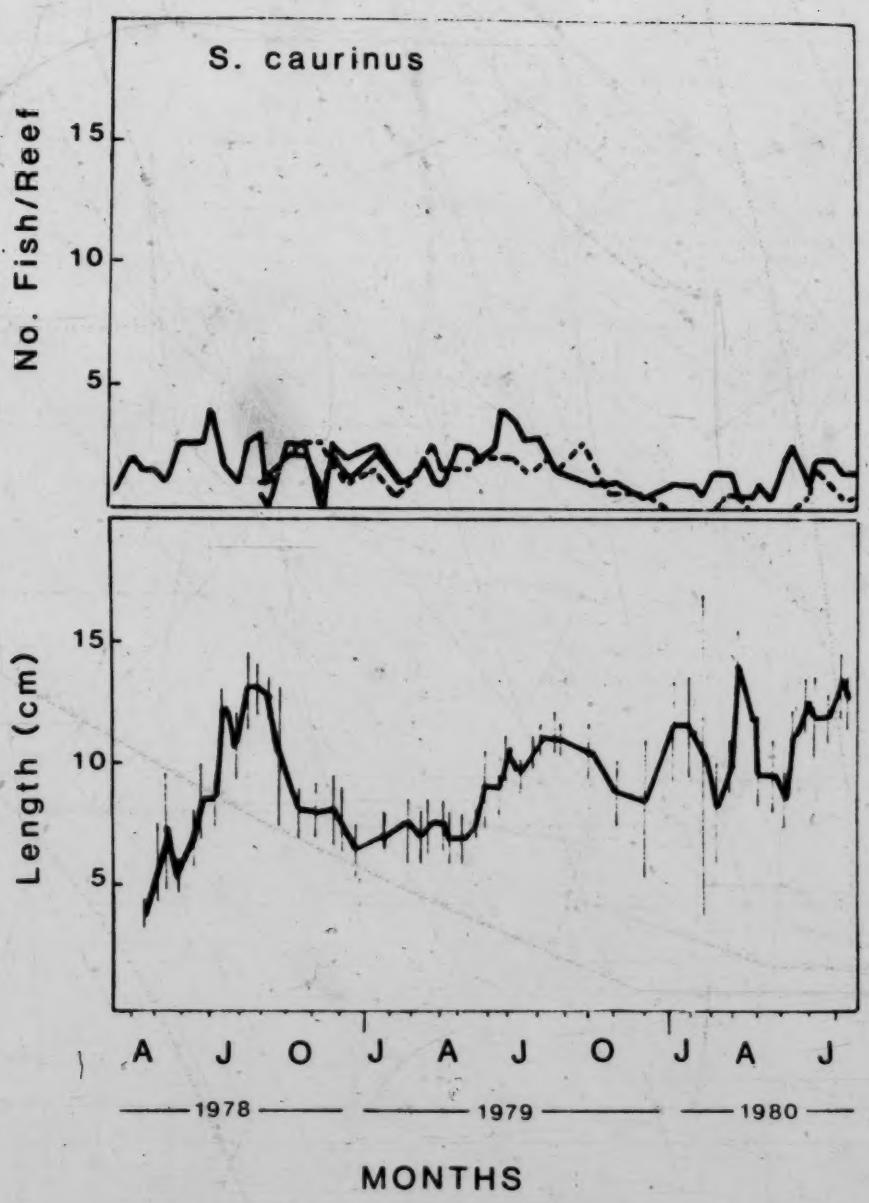

Figure 18: Seasonal changes in the abundance of *Sebastes caurinus* on the artificial reefs. As in Figure 11, the 2 series of insular reefs are pooled. Solid lines: insular reefs; dashed line: continental reefs. The vertical bars around the mean lengths are the 95% confidence limits.

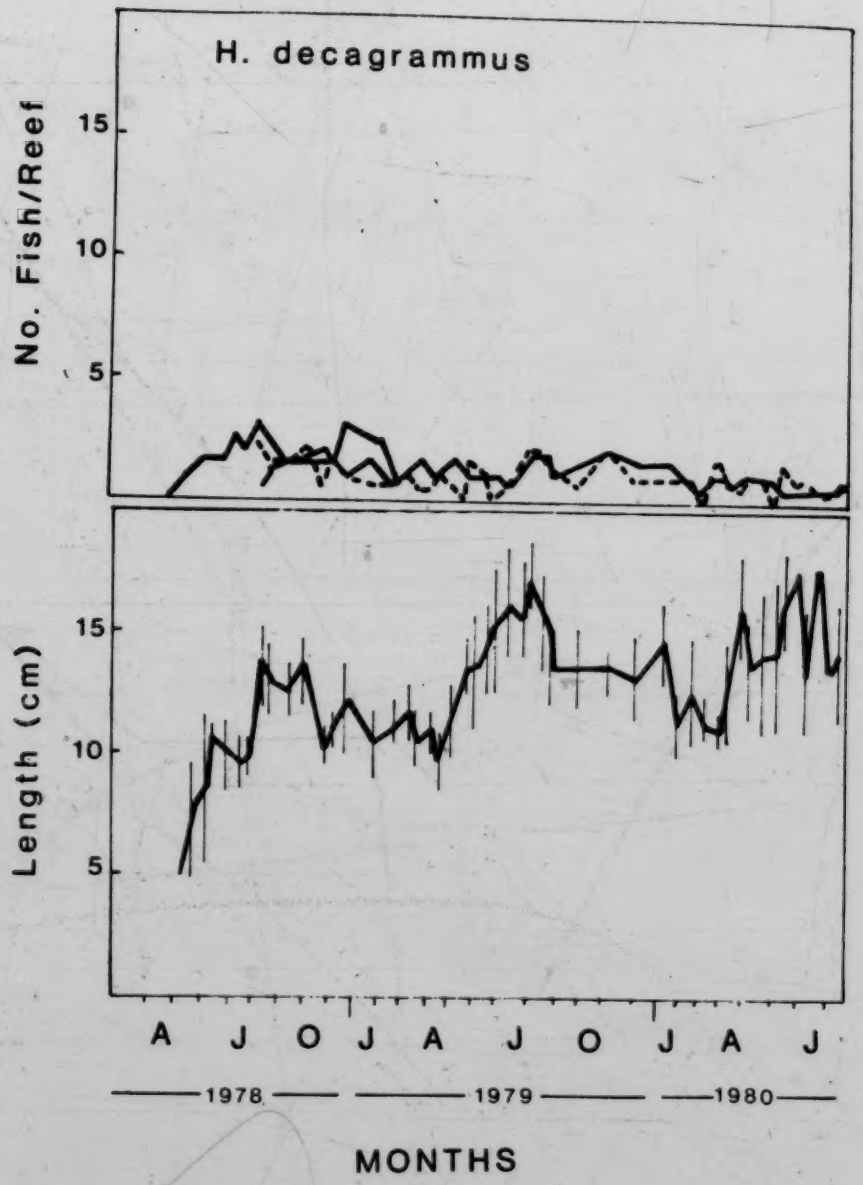

Figure 19: Seasonal changes in the abundance of *Hexagrammos decagrammus* on the artificial reefs. As in Figure 11, the 2 series of insular reefs are pooled. Solid lines: insular reefs; dashed line: continental reefs. The vertical bars around the mean lengths are the 95% confidence limits.

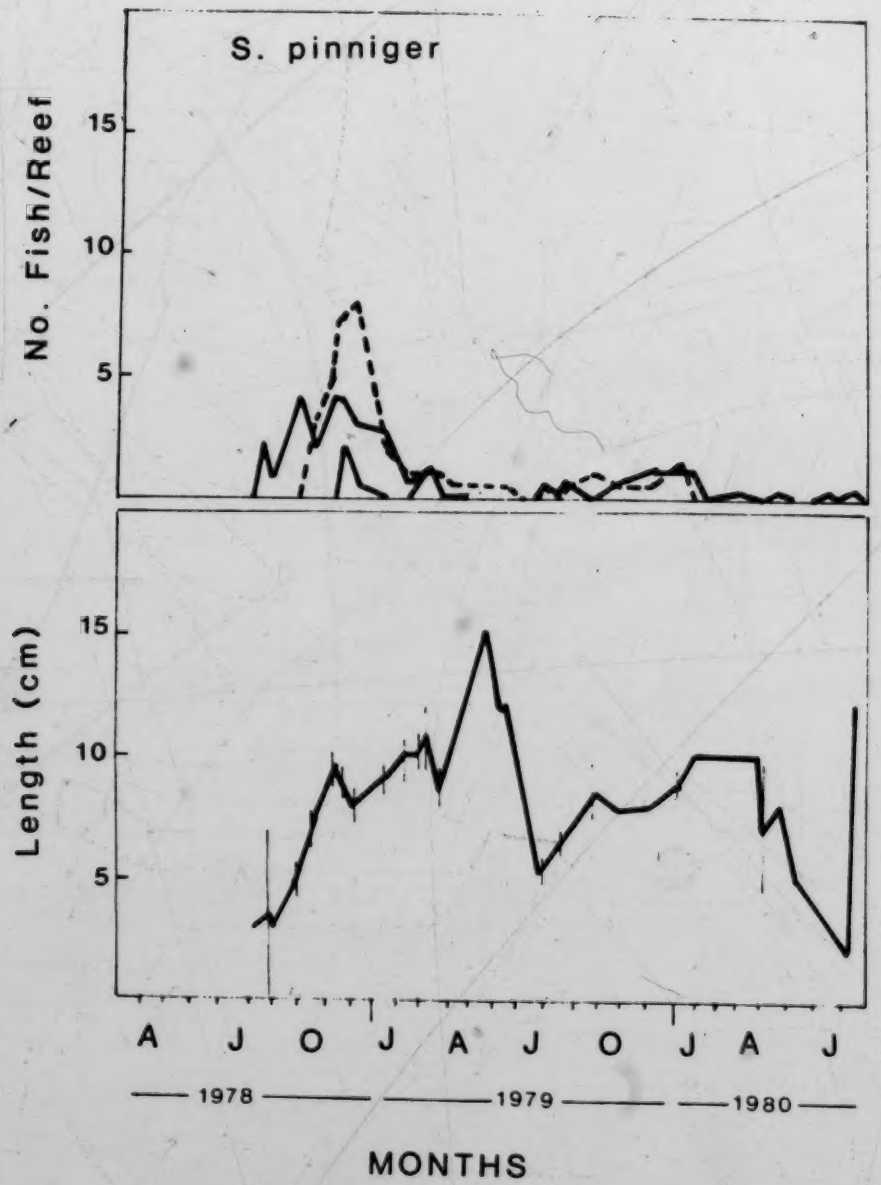

Figure 20: Seasonal changes in the abundance of *Sebastes pinniger* on the artificial reefs. As in Figure 11, the 2 series of insular reefs are pooled. Solid lines: insular reefs; dashed line: continental reefs. The vertical bars around the mean lengths are the 95% confidence limits.

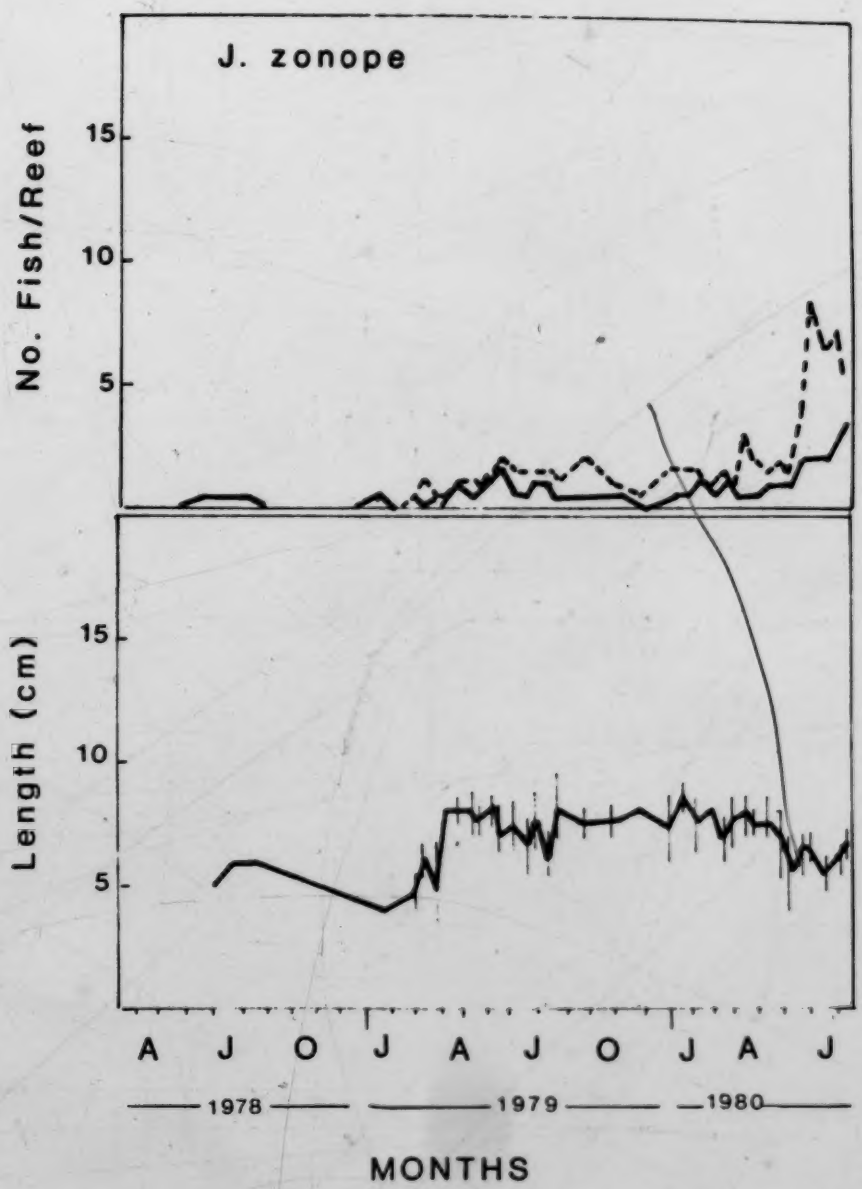

Figure 21: Seasonal changes in the abundance of *Jordania zonope* on the artificial reefs. As in Figure 11, the 2 series of insular reefs are pooled. Solid lines: insular reefs; dashed line: continental reefs. The vertical bars around the mean lengths are the 95% confidence limits.

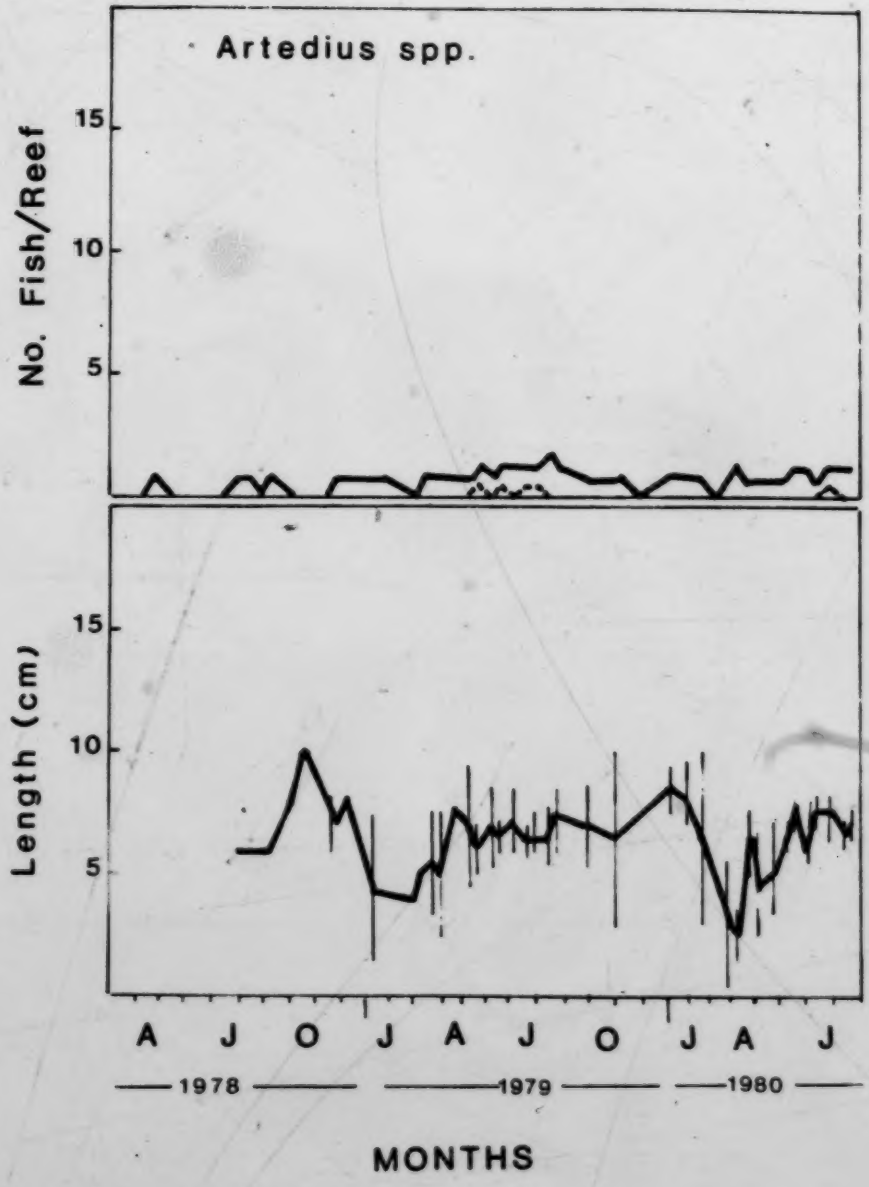

Figure 22: Seasonal changes in the abundance of *Artedius spp.* on the artificial reefs. As in Figure 11, the 2 series of insular reefs are pooled. Solid lines: insular reefs; dashed line: continental reefs. The vertical bars around the mean lengths are the 95% confidence limits.

appearance of large schools of recently metamorphosed juveniles of these two species in summer. These schools were not included in the population estimates, but when they were present, large numbers of solitary individuals of these species were found seeking cover on the reefs. These solitary individuals were counted, since they could not be separated from the resident fishes.

The remaining six species did not show any noticeable seasonal fluctuations (with the exception of *C. nicholsi* on the continental reefs, following the same pattern to that observed on the rock rubble slope), although both *C. nicholsi* and *Jordania zonope* increased in abundance throughout the study (Fig. 15 and Fig. 21).

The demersal species were represented by both adults and juveniles, whereas the rockfish (*Sebastes spp.*) were represented almost exclusively by juveniles. Based on length estimates, and using published growth curves (Leaman, 1976; Moulton, 1977; Six and Horton, 1977), the first 3 year classes of *S. caurinus* and *S. maliger*, the first 2 year classes of *S. melanops*, and the first year class of *S. pinniger* were present on the reefs. The seasonal fluctuations in the mean estimated lengths of these fish on the reefs are plotted in Fig. 15 to Fig. 22 (lower frames). The presence of distinct cohorts is evident in all but *C. nicholsi* and *J. zonope*. The new cohorts of rockfish appeared from June (*S. melanops*, Fig. 16), to August (*S. pinniger*, Fig. 20) and October (*S. caurinus* and *S. maliger*, Fig. 17 and Fig. 18). The reduction in mean length at the beginning of these new cohorts represents the arrival of young of the year on the study site. As the numbers of these species remained relatively constant during the same period (*S. melanops* excepted), it is presumed that the larger individuals (1 and 2-year-old) emigrated. The new cohorts of *Hexagrammos decagrammus* appeared in March-April (Fig. 19) and those of *Artedius spp.* appeared in February-March (Fig. 22). The lengths of *C. nicholsi* and *J. zonope* do not indicate the presence of new cohorts. Large numbers of very small (< 3 cm) *C. nicholsi* were seen in January-February 1980, while similarly small *J. zonope* were noted on the reefs in May 1980. These were presumably recent recruits.

Yearly differences in abundance

Most species showed abundance differences between years. Some only showed slight increases (*C. nicholsi*, *Artedius spp.*, and *Rhamphocottus richardsoni*) which may be related the fact that all are demersal and territorial, thus being slow colonizers. On the contrary, others increased dramatically during the study (*S. auriculatus*, *J. zonope*) (Fig. 23). It is unlikely that these yearly differences resulted from their slow colonization rates, or from biological facilitation (development of an appropriate encrusting community on the reefs). Their numbers were much higher on reef no. 11 in 1980 (which was only few months old, and thus without an encrusting community: see last section) than they were on all reefs combined in 1978. On the contrary, most rockfish appeared to decline in numbers during the study (*S. caurinus*, *S. melanops*, and *S. pinniger*). The absence of the 2 schooling species was very noticeable in 1980. Only few species appeared to remain at a constant level (*S. maliger*, *H. decagrammus*, and *Anarrhichthys ocellatus*).

Duration of residence on the reefs

Eleven fish, belonging to 5 species were tagged on reef no. 4 in 1979; they represented nearly half the fish present at the time. Most of the tagged fish (*S. caurinus*, *S. melanops*, *C. nicholsi* and *J. zonope*) remained for periods of up to 18 months on the reefs. *S. maliger* was an exception, showing a shorter residence time (mean = 99 days, range = 0–229 n = 5). Two of the tagged *S. maliger* were lost immediately after tagging (tag-induced death or emigration?) but the other three stayed for approximately 4 to 6 months (Appendix V).

Community variability

In order to make an estimate of community variability, and in order to make a comparison with the results of Talbot *et al.*, (1978), I repeated their somewhat crude procedure. They compared their reef communities (obtained by combining all successive samples) with each other using the Jacquard index (Goodall, 1978), the so called community coefficient (CC) which is given by:

$$CC = a/a+b+c$$

where a is the number of species in common to both communities and b and c the number of species exclusive to each of the communities. I repeated the same

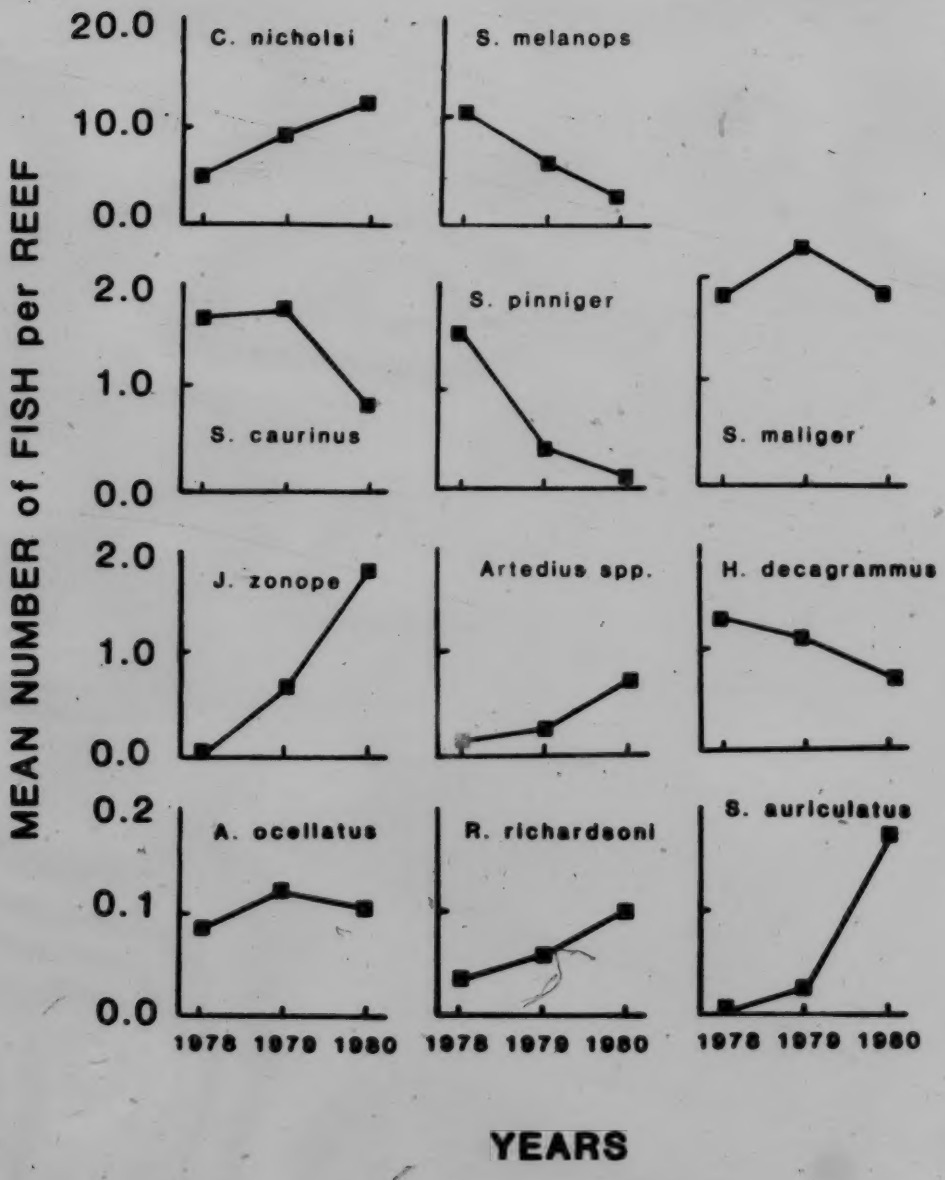

Figure 23: Annual changes in the abundance of the 11 commonest species on the artificial reefs. The values plotted are the mean no. fish/reef averaged over the entire year.

procedure, considering only resident species; the results are presented in Table 6 for all within-series and between series-comparisons. None of these means differed from each other (t-test, $P > 0.05$ in all cases), and the grand mean of **CC** = 0.579 ± 0.036 is much greater than the value of **CC** = 0.342 ± 0.004 reported by Talbot *et al.*, (1978). This procedure ignores both the relative abundance of species and the seasonal elements of community composition, which may be important in the temperate region of Barkley Sound.

In order to consider these two factors, the community composition of each reef was compared to the average community composition in its set of replicates, using a chi-square for the goodness of fit (Table 7). The expected distributions were generated by pooling the observations on all the reefs within a series (i.e. winter insular, summer insular, and continental). Twelve (15 for the winter insular) sets of these average distributions were calculated for the duration of the study, the observations being pooled into two-month intervals (4 consecutive censuses) to avoid counts below 50 (Sokal and Rohlf, 1969). These intervals were short enough to retain seasonal trends, while producing sufficient sample size. Because no values in the expected distributions should be less than 5 (Sokal and Rohlf, 1969), the rare species were pooled. Transients and schooling *S. melanops* were excluded as previously. The community composition of each reef usually did not differ from that of their respective species pool (i.e. average distributions); 47 out of 84 communities (56.1%) were not significantly different from the insular species pool and 21 out of 38 (55%) did not differ from the continental species pool.

Effects of construction time and isolation

Once the summer insular reefs had reached a species equilibrium, no obvious differences could be found between the two series of insular reefs, the relative abundance of the species being similar on both series. Accordingly, the two series were combined after that date.

On the other hand, isolation had strong effects on community development. The species composition was not much affected (no difference was found when only presence/absence data were considered [Table 6]), but the relative abundance of species noticeably differed between the continental reefs and the insular reefs. *C.*

Table 6: Mean community coefficient (CC) for all within and between series comparisons.

Reef community comparison	N	Mean ±95% confidence limits
Within Series		
Winter	6	0.596±0.153
Summer	1	0.721
Continental	6	0.561±0.099
Between Series		
Winter and summer	8	0.606±0.178
Winter and continental	16	0.580±0.059
Summer and continental	8	0.533±0.666
Total	45	0.579±0.036

Table 7: Chi square analysis of the reef fish community structure. Chi-square values. degrees of freedom and their significance levels are given for the comparisons between each reef and their respective species pools (* = 0.05 > p >0.01; ** = p < 0.01).

	Winter insular reefs average distribution				Summer insular reefs average distribution		Continental reefs average distribution			
Reef no.: Time period	1	2	3	4	5	6	7	8	9	10
March-April 1978	8.13 2*	3.53 2	11.64 2**	3.83 1						
May-June 1978	8.16 4	7.35 3	0.37 3	2.59 3						
July-August 1978	14.56 5*	16.61 4**	3.16 4	17.14 4**						
Sept.-Oct. 1978	39.45 4**	20.39 4**	5.29 4	3.43 4	6.27 4	5.48 3	4.51 4	24.53 3**	4.53 4	25.89 4**
Nov.-Dec. 1978	10.39 4*	8.54 4	4.18 4	6.59 4	4.88 4	5.48 1*	12.17 2**	13.67 3**	12.97 3**	18.71 5**
Jan.-Feb. 1979	13.05 3**	6.81 5	6.90 3	6.10 5	5.26 5	5.42 4	4.95 4	8.08 2*	0.14 3	13.96 4**
March-April 1979	7.04 3	4.03 5	1.25 2	10.24 2**	5.19 5	33.74 5**	8.04 3*	1.22 2	2.44 3	11.46 3**
May-June 1979	7.35 3	38.18 6**	7.57 4	9.59 4*	8.42 5	17.00 4**	7.09 5	15.10 4**	3.16 4	21.72 4**
July-August 1979	23.90 5**	24.46 6**	13.96 5**	30.72 5**	73.63 5**	22.24 4**	11.61 4**	12.36 5*	5.67 5	6.89 5

Table 7, continued.

	Winter insular reefs average distribution				Summer insular reefs average distribution			Continental reefs average distribution		
Reef no.: Time period:	1	2	3	4	5	6	7	8	9	10
Sept.-Oct. 1979	15.74 3**	10.15 4*	11.76 4*	10.56 3*	4.72 3	9.39 2**	9.28 2**	14.53 3**	7.36 3	13.47 4**
Nov.-Dec. 1979	13.75 4**	11.46 4*	5.52 2	3.86 3	3.55 4	5.62 1*	 2	2.52	3.00 2	
Jan.-Feb. 1980	11.21 3*	10.41 4*	2.98 2	5.28 3	6.86 3	8.71 4		1.17 4	2.36 1	
March-April 1980		10.93 5	11.37 2**	13.16 2**	10.44 4*	14.26 5**		3.33 2	3.13 2	
May-June 1980		7.34 5	10.17 5	8.03 4*	8.54 4	15.75 4**		3.23 2	1.75 2	
July-August 1980		3.16 5	4.65 5	6.16 4	8.63 5	6.93 5		4.11 4	3.25 4	

nicholsi and *Oxylebius pictus* were 2 to 3 times more common on the continental reefs than on the insular reefs, whereas the rockfishes (*Sebastes spp.*) and the sculpins (Cottidae) were more abundant on the insular reefs. These differences are probably the results of both the dispersal abilities of the species, and habitat differences between the two series of reef (eg. nature of surrounding bottom, depth, etc.).

Effect of position

To detect if position of the reefs within each series had any effect on community composition, correlations between inter-reef distance (in metres) and community similarity were calculated. The community similarity was estimated using 2 indices, community coefficient (CC) as previously, and percent difference (PD). The latter index is to be used extensively in the last chapter and it is one which is recomended by Goodall (1978) as presenting fewest biases. It is given by:

$$PD = \frac{\sum_{i=1}^{S} |Xij - Xik|}{\sum_{i=1}^{S} |Xij + Xik|}$$

where Xij and Xik are respectively the number of species i in community j and k. The correlations were calculated for all the sampling periods used in the previous analysis, and at no time, were the correlations (using both indices) for both series significant. The position of the reefs within each series had no effects on its community composition.

B. Discussion

It is important to consider the patterns (and biases) uncovered in this project in light of what has been already done in coral reef environments. A large part of the work was done by observing the development of communities on isolated patches (Sale and Dybdahl, 1975, 1978; Russell *et al.*, 1974; Talbot *et al.*, 1978; Molles, 1978; Bohnsack and Talbot, 1980); Table 8 presents a summary of the experimental approaches used in these studies. Except for small differences due to local conditions, the designs were similar, and the difference that may exist between

Table 8: A comparison of the experimental procedures used in the studies involving small artificial reefs.

Source	Structures built of	Number of units[1]	Size (cm)	Distance between units (m)	Distance to neareast natural structure
Sale and Dybdahl (1975)	Coral	2 x 10	20-30 (Diameter)	2	??
Talbot *et al.* (1978)[2]	Concrete blocks	8 x 2	160 x 60 x 60	15	10
Bohnsack and Talbot (1980)[2]	Concrete blocks	8 x 2	160 x 60 x 60	15	10
Molles (1978)	Concrete blocks	4 x 3	117 x 38 x 57	15	15
Present study	Concrete blocks	2 x 4 1 x 2	240 x 60 x 90	10	10

1: Number of experimental treatments x no. units per treatment.
2: The experimental designs were the same in these two studies.

Table 8: Continued.

Source	Water depth[3] (m)	Time span (months)	Number of species	Location
Sale and Dybdahl (1975)	0.7(LT) 3.0(HT)	24	56	Australia
Talbot *et al.* (1978)	3-5	30	105	Australia
Bohnsack and Talbot (1980)	3-5	30	89	Florida
Molles (1978)	4.9-5.8 (LT)	18	57	Sea of Cortez
Present study	5-9(LT) 9-12(HT)	30	35	Barkley Sound

3: (LT): low tide; (HT): high tide.

Barkley Sound and the tropics cannot be attributed to differences in design.

In this study, as in all others listed in Table 8 (with the exception of the work of Sale and Dybdahl [1975, 1978]), the estimations of fish population were done visually. Unfortunately, this procedure underestimates the abundance of cryptic or nocturnal species (such as Stichaeidae, Pholidae, Cyclopteridae, and some Cottidae). Leaman (1980) collected large numbers of these species in his poison stations from Barkley Sound. The poisoning done on the rock rubble slope indicates that this cryptic component is very small in the Ross Islets study site (see Chapter III). Smith and Tyler (1972) and Bohnsack (1979) discussed the bias involved in visual censusing of reef fish communities, as opposed to chemical collections. Both techniques differentially underestimate part of the communities, although the patterns observed by one technique are usually apparent in the samples obtained by the other. Smith and Tyler (1972) concluded that visual censuses were overall more effective. Sale and Douglass (1981) estimated the efficiency of visual censuses at 60-80% on coral patches. Efficiency on the structurally much simpler artificial reefs is probably in the upper range of their estimate.

Systematic destructive sampling, using an ichthyocide, was precluded by the design and goals of the experiment. An attempt to poison three reefs, when reef nos. 1, 7, and 10 were dismantled to make room for new structures, failed because of the low water temperature (6°C) and the presence of a slight current at the time. This lapse will not affect the interpretation of the results, as all previous studies were also conducted visually, and thus subject to the same biases.

The communities inhabiting the reefs had a low diversity of species, 8 of them forming 96% of the resident fishes. These 8 species were also the commonest species on the rock rubble slope (see Chapter III). The remaining 19 species were too rare to allow the distinction of any patterns; since these other species were all as small as the common ones, and of the same trophic level (eg. microcarnivores), it is doubtful that they had a strong functional significance in the community.

Not only did the reefs not exclude any of the species present on the transects, but the densities of fish were similar (or slightly higher on the reefs). While it is reasonably straightforward to estimate density on the relatively flat transects, it is

very difficult to do the same on the reefs, due to the inherent difficulty of estimating the area of a three-dimensional structure. The basal area of the reefs was 1.44 m^2. This is certainly an underestimate of the area available to fish (eg. area available inside the blocks). The area of the faces of the reef pyramids is probably a superior estimate, conceptually closer to the area measurements taken on the transects. This estimate gives an area of 4.5 m^2 for the reefs. The number of fish on the reefs usually did not exceed 30, yielding an estimate of density between 7 fish/m^2 to 20 fish/m^2, the lowest estimate (based on the largest area measurement) being slightly higher than the maximal density of 4-5 fish/m^2 found on the rock rubble slope (Chapter III).

In addition, the area available for the different species may not have been the same. For example *J. zonope* rests mostly against vertical surfaces (personal observation) and the rather sharp vertical elevation of the reefs provides large areas of vertical surfaces available for it. On the other hand, *C. nicholsi* uses mostly flat horizontal surfaces on the reefs – the surrounding sand at the base and the ledges – and the area that *C. nicholsi* can use is probably closer to the lower estimate (1.44 m^2), plus a portion (impossible to estimate accurately) of the sandy area surrounding the reefs. This may explain why *J. zonope* is relatively more abundant on the reefs than on the transects, while the opposite is true for *C. nicholsi*.

A great degree of temporal stability is visible in this system. The mean number of species per reef remained remarkably constant throughout the study, and if one examines each reef individually, the pattern remains the same (Appendix III). This apparent lack of seasonality is surprising, considering that Molles (1978), working at a lower latitude in the Gulf of California, was able to detect strong seasonal fluctuations in the number of species, whereas Talbot *et al.* (1978), working under even more tropical conditions, reported strong and erratic fluctuations. Although the number of species remained constant throughout the year, the kind of species changed faster in summer as both the immigration and emigration rates increased then. Most of the sightings of the rarer species were made in summer, and these rare species accounted for most of the increase in turnover.

The number of fish on the reefs did vary seasonally in a fashion similar to that reported by Molles (1978) and Talbot *et al*. (1978). These changes were almost entirely caused by fluctuations in abundance of the schooling rockfish (*S. melanops* and *S. pinniger*), the peaks of these two species being the result of the massive settlement of young of the year during a brief and well-defined period of time. Recruitment in the other species was never as massive as in these two species of rockfish, nor did they show any patterns of seasonal abundance. Nevertheless, some species fluctuated around the mean value (eg. *S. caurinus, S. maliger*) throughout the year. On the reefs most of the fish, with the exception of the two schooling rockfish and of *C. nicholsi* on the continental reefs, did not show seasonal fluctuations, which was surprising because they did show a seasonal pattern on the rock rubble (Chapter III). This could have been partly the result of the greater structural simplicity of the reefs, allowing more readily the detection of fish which had sought cover on the reefs (because of low temperature, turbulence, etc.), yet *C. nicholsi* fluctuated on the continental reefs in parallel with its fluctuation on the rock rubble. These differences between the rock rubble slope and the reefs may be depth-related. Temperature was uniform throughout the study site in winter. On the other hand, turbulence may have been responsible, but except for the upper 2 or 3 m, it was hardly perceivable on the transects, or where the reefs were located. However, I noticed that many fish (especially *S. melanops*) would always be found under cover following heavy seas, and that they would remain there for several days. We never dove on the study site during stormy weather, but it may be that the difference in turbulence between the transects and the reefs during these storms was sufficient to account for the changes in fish behaviour between the two areas.

Individual fishes remained on the reefs for long periods of time. The results of the tagging, confirming previous studies (Love, 1979), indicated association with the reefs ranging from two months to at least nine months. Qualitative observations that I made at night showed that the fish remained on the reefs throughout the 24 hours of the day. The tagged rockfish were seen on their reef at night, indicating that they were not using these structures as a daytime resting place only. While the nocturnal behaviour of rockfish did not appear different from their diurnal behaviour, other

species (*C. nicholsi*, *H. decagrammus*) became quiescent and were invariably found hiding in holes at night.

The duration of stay of some of the rockfishes seems to be limited by well-timed migratory movements by the populations of demersal rockfishes. The cohort replacement in these species showed that their populations turned over almost entirely in the fall. Adults of these fishes were never seen on the study site, although they are commonly found in deeper reefs (Moulton, 1977; personal observations). This migratory ability may explain why rockfishes colonized the reefs more rapidly than the demersal species (eg. *C. nicholsi*, *J. zonope*).

The fish communities were very uniform. The similarity between units, as measured by the community coefficient (**CC**), was almost twice the mean **CC** reported by Talbot *et al.* (1978) [0.579 *vs* 0.342] who were working at the southern end of the Australian Great Barrier Reef. The variances of these estimates of variability differ considerably (confidence limits of ± 0.036 *vs.* a value of ± 0.004 for Talbot *et al.*). Talbot *et al* (1978) are extremely unclear on how they arrived at this value – except for mentioning that they pooled all censuses together. If they calculated an average of their census mean values, instead of the mean **CC** between the global species pool present on the reefs, the difference would be accounted for (because of their larger sample size), although the calculation of the confidence limits would be inappropriate (because a lack of independence between successive censuses). However, if such were the case, these values would not be comparable, their mean greatly underestimating the similarity in the global species pool on their reefs.

The comparison is further complicated by the fact that they used four different types of reef, introducing a between-habitat variation in their measure. Unlike their reefs, and those of Molles (1978), all the ten original reefs were identical in this study. The reefs used by those authors differed in the sizes and combination of openings available. Talbot *et al.*, concluded that these factors were responsible for only a small proportion of the observed variability between their units, the mean community similarity between their similar units (**CC** = 0.367) being still considerably lower than that obtained in this study.

The lack of significant correlation between community similarity and inter-reef distance indicates that no major environmental gradient, at least as perceived by the fish, existed along the study site. The study site was selected for its apparent environmental homogeneity so that truly replicated communities could be established, although it is impossible *a priori* to know how the fish will perceive the environment. In spite of this environmental (along the study site) and habitat (the reefs being identical) homogeneity, the communities inhabiting the reefs were surprisingly heterogeneous (45% of the reef communities differing from their respective species pool), the number of species remaining the same, but the number of individuals for any species varying. This heterogeneity is difficult to interpret biologically. It may indicate that the developmental history of each of the communities on these homogenous habitat patches may have been quite different, indicating a great deal of stochasticity in the colonization process itself.

However, in environmentally heterogeneous conditions (for example between insular and continental reefs) selection was clearly evident, a fact attested by the differences between the communities on these two series of reefs. As well as distance from shore, three factors are potentially responsible for the difference: depth (small difference of 2-3 m), isolation, and the nature of the bottom surrounding the reefs (sand *vs* a mixture of sand and rocks). It is impossible to assess the relative importance of each factor from the present data, as they always covary.

The two demersal and territorial species, *C. nicholsi* and *J. zonope* (Wiley, 1973; Leaman, 1980; K.S. Cole, personal communication) were more abundant on the continental reefs, whereas the remaining species were more abundant (in absolute numbers) on the insular reefs. The lower abundance of *C. nicholsi* and *J. zonope* on the insular reefs is probably a result of low dispersal abilities, a fact hardly surprising considering their territoriality and attachment to a home site. The greater absolute abundance of the other species on the insular reef cannot be directly a function of the dispersal potential of these species, although the speed at which many of these species fully colonized the reefs (eg. *S. maliger, S. caurinus*) indicates that they are better dispersers than the territorial fishes. Depth differences (of a few metres) between the two series of reefs may account for some of this, as many rockfish are more abundant in deeper waters (Moulton, 1977; personal observations), but the little

difference in depth that existed seems hardly sufficient to explain the large differences in abundance (eg. insular:continental ratios for *S. maliger* = 4:1; *S. caurinus* = 2:1; *Artedius spp.* = 14:1).

The lower abundance of the two territorial species may have favoured the abundance of the rockfishes on the insular reefs, but this is very tenuous evidence for competition. *C. nicholsi* and *J. zonope* increased in abundance on the reefs throughout the study, while *S. caurinus* decreased. Yet, the two territorial species seem to have affected only the spatial distribution of *S. maliger* on the reefs, *S. maliger* remaining relatively constant in numbers on the reefs throughout the study, while they did not interact with *S. caurinus* (Chapter V). Furthermore, the sculpins (*Artedius spp.*) were almost entirely restricted to the insular reefs, yet they increased in abundance on the insular reefs in parallel with *C. nicholsi* and *J. zonope*. Some of the differences between the insular and continental reefs may then be due to the differing successional stages of the two systems. Clearly, the evidence is very weak, and long term experimental studies are required to determine whether a long term succession is proceeding on the reefs.

Finally, factors associated with the isolation of reefs on sand may be responsible for attracting some fish to the reefs. The rockfish speared in 1980 had fed on schools of small fishes (*Clupea?, Engraulis?*), and if these schools are restricted to sandy habitats, as they appeared to have been (we never saw them on the two rock rubble transects), some of the fish may be attracted to this rich food source. Space (or shelter) is often assumed to be the factor attracting fish to reef and this may be true for some species (see Chapter V), although not for all of them. Further work is required to determine what resource ultimately attracts fish to habitat, and artificial habitats will provide an elegant experimental technique.

On the other hand, time of construction had little influence on community composition. Recruitment to the community is highly seasonal, the periods of recruitment (i.e. appearance of newly metamorphosed fish) being spread from February to October. This strong seasonal factor had led me to postulate that it might affect community development, as it did for fouling communities (Sutherland, 1974). Contrary to what happens in the tropics where recruits to isolated patches are almost

exclusively of planktonic origin (Sale, 1977; Russell *et al.*, 1978), the colonists to the reefs appeared to be mostly adult or subadult fishes; settling larvae from the plankton were never seen in great abundance on the reefs. It is impossible to know exactly what proportion of the colonists were coming from the surrounding habitats (as opposed to the plankton), but all the fish seen immediately after construction (i.e. recent colonists) were such. The community development is thus probably only weakly tied to recruitment.

The yearly differences in abundance mentioned earlier are certainly in part the result of varying recruitment. Year class strength (i.e. number of surviving young produced) is quite variable in many marine fish species (Cushing, 1975). The overall abundance of many of these species (*S. melanops, S. pinniger, S. auriculatus, J. zonope,* and *Artedius spp.*) varied from year to year on the study site (reefs + transects + qualitative observation on the rest of the area; see section on yearly differences) and the difference observed on the reefs seem to reflect more general conditions on the study site. These fluctuations usually involved young of the year (all four rockfishes), which may indicate a large degree of density independent regulation of these populations (Cushing, 1975).

In conclusion, the artificial reefs provide an excellent means of studying, in an controlled fashion, the reef fish community inhabiting the rock rubble habitat, as both the species composition and densities on the reefs were similar to that of the rock rubble slope. Some differences existed, and some seem to have been attributable to habitat differences. In the next chapter, I will examine some of the factors that control habitat selection by these fishes.

V. RESULTS III:

Mode of habitat use on the artificial reefs

Living space is commonly acknowledged as limiting many populations of tropical reef fishes (Sale, 1980b), and the little information available from temperate regions seems to indicate this may also be the case at higher latitudes (Ebeling and Bray, 1976; Larson, 1980a, 1980c). Artificial reef studies have shown that new space is normally occupied very rapidly (Turner *et al.*, 1969; Chapter IV) indicating that the availability of living space is also important for temperate reef fishes. Furthermore, the presence of shelter has been shown to be crucial for many reef species (Stephens *et al.*, 1970; Olla *et al.*, 1979; Phillips and Swears, 1979). Two important factors controlling microhabitat selection have been identified as vertical relief (Gosline, 1965; Gibson, 1972; Terry and Stephens, 1977; Hixon, 1980; Larson, 1980a) and shelter type and size (Haines and Butler, 1969; Stephens *et al.*, 1970).

Nevertheless, the exact microhabitat requirements of fish are usually not defined, and the factors influencing space use are generally unknown. This may be a consequence of the difficulty of categorizing and quantifying habitat, in other than subjective terms (Luckhurst and Luckhurst, 1978b). On the other hand, categorization of microhabitats on artificial structures made of concrete blocks is easier, since they are made of uniform and well defined units. Thus the basic components controlling microhabitat selection can be more easily identified on such structures. Many species present in this system are of considerable interest in recreational fisheries (eg. *Sebastes spp.*) and a detailed knowledge of their spatial requirements would greatly enhance our ability to design large commercial artificial reefs capable of attracting them (see review by Stone, 1978).

In addition to adaptations (either morphological or behavioural) by the fish to specific types of habitat, interactions between the species may affect their utilization of space. Interspecific competition is one of such factors; Larson (1980a) has experimentally demonstrated that interspecific competition in a pair of rockfishes (*Sebastes carnatus, S. chrysomelas*) greatly affected their spatial distribution. The effects of competition generally result in greater niche separation (Werner and Hall, 1976; Diamond, 1978; Hixon, 1980; Larson, 1980a), the so-called "niche overlap

hypothesis" of Pianka (1972). Predation is another powerful force and can potentially greatly affect the spatial distribution of fish species, although it is not clear *a priori* what the effects might be.

In this chapter, I examine the patterns of microhabitat use and spatial separation among the fishes inhabiting the artificial reefs. Furthermore, I examine the hypothesis that if interactions between, or within species, affect space use, significant shifts in the spatial distribution with increases in density (taken here as an estimator of the strength of these potential interactions) will occur within the reefs. The two variables specifically considered are shelter type and elevation above the substratum (vertical relief).

A. Analytical methods

Habitat selection was measured with Ivlev's index of electivity (Ivlev, 1961). This index, originally proposed for food studies, can be applied to any kind of resource for which availabilities are known. Electivity is given by:

$$E_i=(p_i-R_i)/(p_i+R_i)$$

where p_i is the proportion of resource i used, and R_i its proportion in the environment. The index varies from −1 (total avoidance) to +1 (absolute selection). Electivities for the large holes are likely to be overestimated, because the counting procedure underestimated their availabilty (by ignoring area).

In order to determine if significant shifts in space use occurred with changes in the density of potential competitors, I built 3-dimensional contingency tables (Fienberg, 1970; Colgan and Smith, 1978). The two habitat variables, hole type [H] and row elevation [R] were considered against the density of fish on the reefs [D]. The technique involves working through a series of log-linear models predicting expected cell frequencies, in order to find the model with the least number of terms, which fit the data (Colgan and Smith, 1978). The models are hierarchical, requiring that when an interaction term is included, all lower terms involving the same variables are also included. The goodness of fit of the model with the data is tested with the likelihood X^2 statistics. Due to its additive properties, the difference between the X^2 of two models differing by only one term is a test of the significance of that term to the

model; thus it is called a test of partial association (Brown, 1976). Following Colgan and Smith (1978), once a model is selected, the partial association of its terms are tested, and those that do not contribute significantly to the fit of the model deleted. However, this never happened in this study. I gave the partial associations only for the three way interaction term [DRH], as the expected frequencies of the saturated model are by definition the observed values ($X^2 = 0$; df = 0) (Colgan and Smith, 1978), and thus no significance can be attached to the model itself. For greater details, the reader is referred to the papers by Fienberg (1970), Jenkins (1975), Brown (1976), and Colgan and Smith (1978).

For each of the considered species, a series of 3-dimensional tables were built, each one representing space use against up to five density categories of a different species (Table 9). The tables for each density category were constructed by pooling all observations (independently of reef or census) falling into that density interval. The limits of the density categories were chosen so that the number of observations in each were approximately equal. However, examination of the original expected frequencies in the tables forced me to do some consolidation of the categories on the density dimension. The limits of the final categories are given in Table 9. They are not identical from species to species, since all the species were not equally abundant. The tables were analysed with the program P3F (Multiway Frequency Tables) in the BMDP package (Dixon and Brown, 1979).

In the following discussion, the models are identified in the usual manner (see Colgan and Smith, 1978) by using a code letter to represent the variables (hole: [H]; row: [R]; density: [D]). Thus, the model [D,R,H] indicates that only the main effects are present and that all the variables are independent. In the model [DR,DH], two interaction terms are present ([DR] and [DH]), meaning that the factors in these 2 terms (D and R, D and H) are not independent of one another. The main factors ([D],[R],[H]) are also present (because of the hierarchical nature of the models), but they are usually not written down, as their presence is implied by the interaction terms ([DR],[DH]). Because of the large number of models tested, I used a significance level of 1% to minimize type I error.

Table 9: Limit of the abundance classes for the multidimensional contingency table.

Species	Abundance classes				
	0	1	2	3	4
C. nicholsi	0	≤ 5	≤ 8	≤ 11	>11
S. melanops	0	1	2	≤ 6	>6
S. maliger	0	1	2	≤ 6	>6
S. caurinus	0	1	≤ 3	>3	
H. decagrammus	0	1	>1		
J. zonope	0	1	>1		
S. pinniger	0	≥ 1			

B. Results

Of the 50 species recorded on the reefs, 8 were common enough to be studied closely (Table 10). Most species were seen both as adults and juveniles, with the exception of the rockfish (*Sebastes spp.*) which were seen only as juveniles. The sculpins of the genus *Artedius* are extremely difficult to distinguish visually underwater and thus the 3 species found are considered together; *A. fenestralis, A. harringtoni,* and *A. lateralis* were all collected from the study site so the grouping *Artedius spp.* probably includes them all. Only two species, *Sebastes melanops* and *S. pinniger,* showed regular seasonal fluctuations (Fig. 16 and Fig. 20). The remaining species fluctuated around a mean value without showing any evidence of regular annual cycles, although some (*Coryphopterus nicholsi, Jordania zonope*) were distinctly more abundant in some years (Fig. 15 and Fig. 21).

Association with the reefs

Most fish were in close association with the reefs and could be easily assigned positions (Table 10), but a large proportion of *S. melanops* (61.3%) and *S. pinniger* (15%) occurred in small aggregations around or above the reefs. The fish in these aggregations seemed to associate with the structures, although they could not be assigned a specific position on the reef surface.

Microhabitat selection

I combined all observations, regardless of reef and census to measure the microhabitat use by the different species (Fig. 24). The requirements of all species were quite specific, each showing selection on the two variables investigated. Their distribution always differed significantly from what would have been expected, had they each used the habitat types in the proportion to their availability (X^2 for goodness of fit, $P < 0.01$ in all cases).

The non-rockfish (i.e. benthic species) species can be grouped into two categories. *C. nicholsi* and *H. decagrammus* were found mostly at the lower levels on the reefs, while *Artedius spp.* and *J. zonope* were found mostly on the upper rows.

The rockfish could also be divided into two groups. *S. caurinus* and *S. maliger* were always found in contact with the blocks. Their patterns of microhabitat

Table 10: List of the 8 most common species of fish on the artificial reefs, with size range, and the proportion of those sighted in close contact with the reef structure, as opposed to those seen swimming around them.

Species	Total	size (cm.)	Contact (%)	Swimming (%)
Coryphopterus nicholsi	2027	3-12	99.4	0.6
Sebastes melanops	1661	6-15	38.7	61.3
Sebastes maliger	783	4-15	98.8	1.2
Sebastes caurinus	490	4-20	98.4	1.6
Hexagrammos decagrammus	314	6-35	93.3	6.7
Jordania zonope	157	2-12	100.0	0.0
Sebastes pinniger	154	4-15	85.1	14.9
Artedius spp.	153	2-10	100.0	0.0

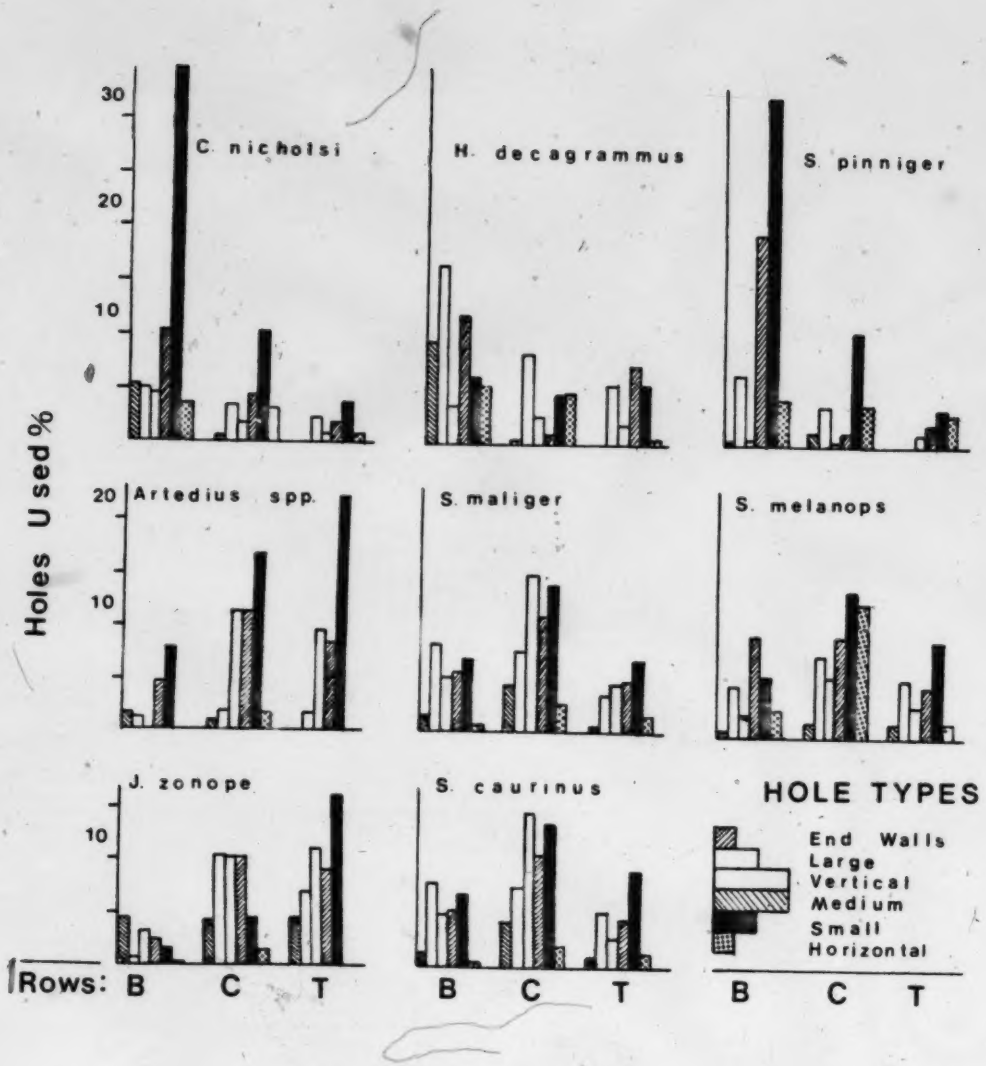

Figure 24: Microhabitat use by the 8 common species expressed as the proportion of fish (%) in each habitat category (holes x rows).

use were almost identical; they were concentrated at intermediate elevation on the reefs (Fig. 24). The two pelagic rockfish were the only ones to make consistent use of the open waters surrounding the reefs. They were separated in the vertical dimension, *S. pinniger* being most common on the lowest row , whereas *S. melanops* was more abundant in the centre row (Fig. 24).

Each species selected for approximately one third of the possible microhabitat categories (6–8 out of 18 positive electivities, Fig. 25). The demersal rockfishes (*S. caurinus* and *S. maliger*), *H. decagrammus*, and *J. zonope* used the larger holes, whereas the remaining benthic species and the two pelagic rockfish (*S. pinniger, S. melanops*) selected smaller ones.

Community effects on microhabitat selection

Five species (*C. nicholsi, H. decagrammus, S. caurinus, S. maliger,* and *S. melanops*) were abundant enough to test the effects of changes in the density of other species on their space use. Space use was tested against the density of all species from Table 10, with the exception of *Artedius spp.*, which represents a mixture of at least three species. All the fitted models (i.e. the significant model with the least interaction terms), testing the space use of the 5 common species against changes in the density of 7 potential competitors, are given in Table 11. The presence of DR or DH interaction terms in the fitted model (statistical dependence of row use or hole use on density) was taken as indicating significant shifts in space. These shifts are schematically represented in Figs. 26 and 27.

The space utilization of *S. melanops* was dependent on the abundance of each of the other species, with the exception of *S. caurinus*. Its changes in space use against increases in the density of two benthic species (*C. nicholsi, H. decagrammus*) consisted of an increase in its use of the upper rows and smaller holes (Fig. 26a, 26d). When the histograms from Fig. 26 are compared to those of Fig. 24, it becomes apparent that the direction of these changes produced a small increase in space separation, as theoretically predicted, with respect to elevation against *C. nicholsi* and *H. decagrammus*, as these two species were more abundant on the lower row (Fig. 24). Its increased separation with *H. decagrammus* was also achieved on the basis of hole type, as the latter used mostly the larger holes (Fig. 24). The

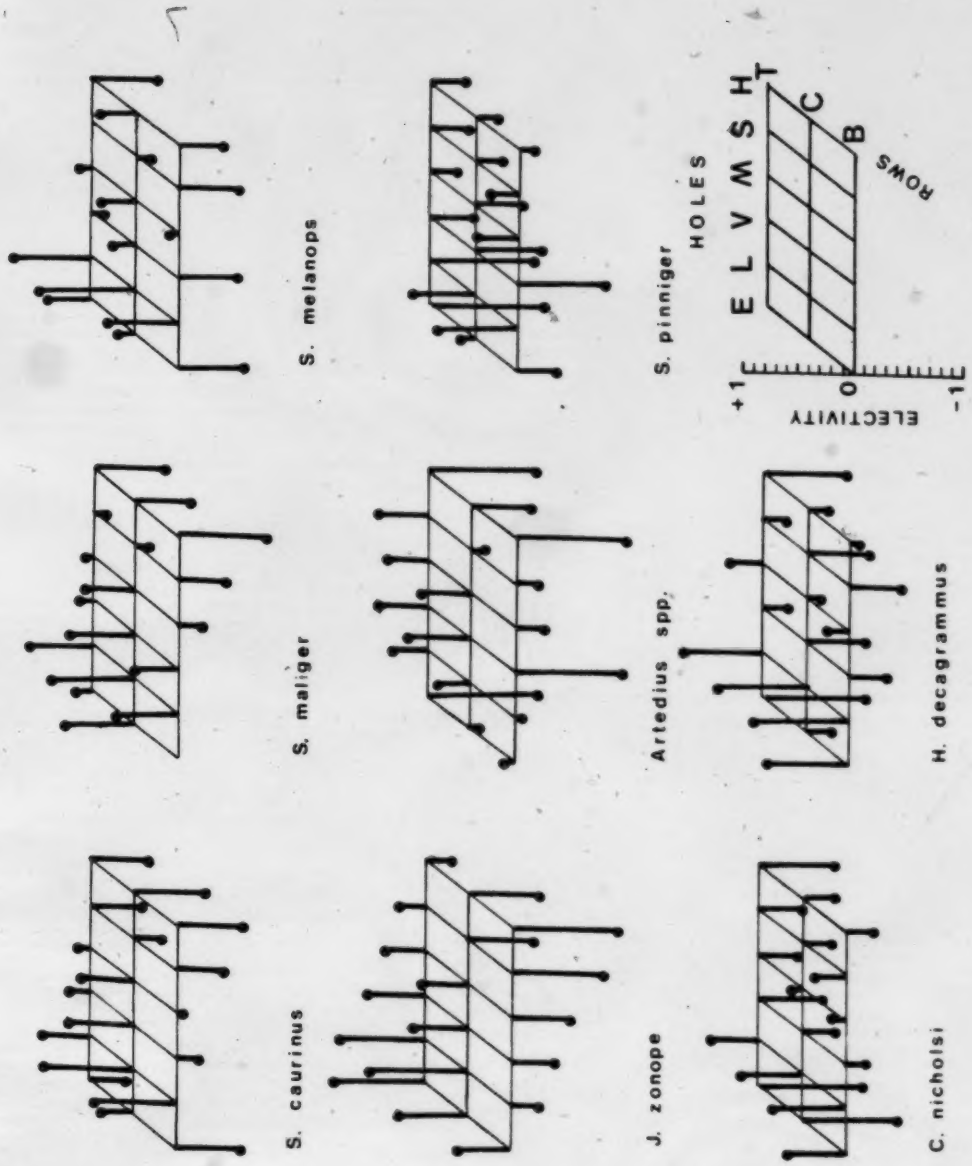

Figure 25: Microhabitat selection (Ivlev's electivities) by the 8 common species. The points above the plane indicate habitat categories selected for (E > 0), whereas those below represent categories selected against (E < 0). Abbreviations: E: end walls; L: large holes; V: vertical holes; M: medium holes; S: small holes; H: horizontal holes; T: top row; C: centre row; B: bottom row.

Table 11: Fitted models for each of the 35 species pairs. The models are the simplest models (i.e. with the minimum no. of interaction terms) that produced expected values that did not differ significantly ($p > 0.01$) from the observed space use. Since the expected values of the saturated model [DRH] are by definition the observed values, the test of partial association (Part. ass. [DRH]) of the 3-way terms are given under the model, including the probability level indicating the lack of fit ($p < 0.01$) resulting from their deletions. The models which include an interaction term involving density are indicated in boldface.

	Test for the goodness of fit:			
	Model	X^2	df	P
Response of *Coryphopterus nicholsi* to increases in the density of:				
C. nicholsi	**[DR,DH,RH]**	33.40	40	0.3054
S. melanops	[RH,D]	96.85	68	0.0123
S. maliger	[RH,D]	76.73	68	0.2191
S. caurinus	[RH,D]	66.87	51	0.0671
H. decagrammus	**[DR,RH]**	36.79	30	0.1834
J. zonope	[RH,D]	39.52	34	0.2370
S. pinniger	**[DRH]**	0.00	0	
	(Part. Ass. of [DRH] term	24.10	10	0.0073)
Response of *Sebastes melanops* to increases in the density of:				
C. nicholsi	**[DRH]**	0.00	0	
	(Part. Ass. of [DRH] term	74.71	40	0.0007)
S. melanops	**[DR,DH,RH]**	36.61	30	0.1127
S. maliger	**[DH,RH]**	62.04	48	0.0838
S. caurinus	[D,RH]	73.56	51	0.0210
H. decagrammus	**[DRH]**	0.00	0	
	(Part. Ass. of [DRH] term	52.15	20	0.0001)
J. zonope	**[DR,DH,HR]**	36.74	20	0.0126
S. pinniger	**[DR,DH,RH]**	15.44	10	0.1167
Response of *Sebastes maliger* to increases in the density of:				
C. nicholsi	**[DRH]**	0.00	0	
	(Part. Ass. of [DRH] term	67.60	40	0.0041)
S. melanops	[D,R,H]	104.77	78	0.0244
S. maliger	[D,R,H]	70.34	61	0.1933
S. caurinus	[D,R,H]	72.66	61	0.1458
H. decagrammus	[D,R,H]	61.54	44	0.0414
J. zonope	**[DR,DH]**	43.68	30	0.0510
S. pinniger	[D,R,H]	36.54	27	0.1040
Response of *Sebastes caurinus* to increases in the density of:				
C. nicholsi	[D,R,H]	81.95	78	0.3579
S. melanops	[D,R,H]	76.63	78	0.5257

Table 11: continued.

	Test for the goodness of fit:			
	Model	X^2	df	P
J. zonope	[D,R,H]	59.92	44	0.0552
S. pinniger	[D,R,H]	28.37	27	0.3432
Response of *Hexagrammos decagrammus* to increases in the density of:				
C. nicholsi	[R,H]	80.24	82	0.5343
S. melanops	[R,H]	98.52	82	0.1032
S. maliger	[D,R,H]	93.11	78	0.1167
S. caurinus	[D,R,H]	89.49	64	0.0102
H. decagrammus	[RH,D]	26.00	17	0.0744
J. zonope	[D,R,H]	66.11	44	0.0171
S. pinniger	[RH,D]	18.61	17	0.3512

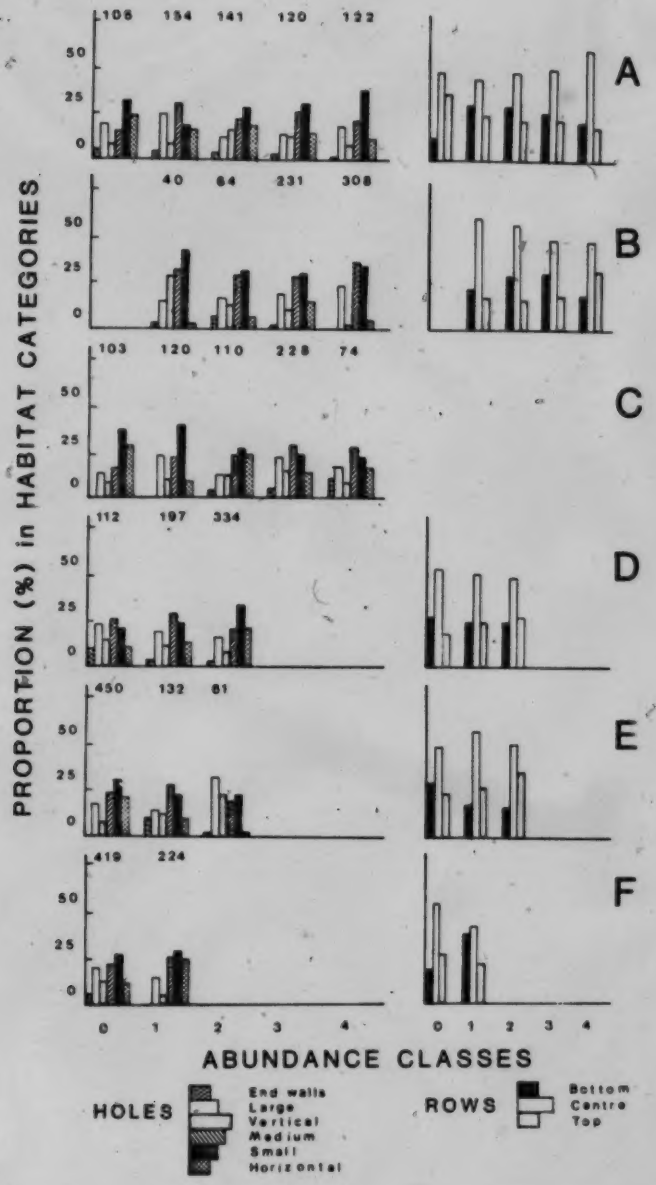

Figure 26: Effects of density on the space utilization of *S. melanops*. In each figure, the bar histograms represent hole utilization (left column) and row utilization (right column) at different densities of other species (for the definition of the abundance classes, see Table 11), whenever a [DR] or [DH] interaction term was present in the fitted model (i.e. significant effects of density). Number of observations at each density level are given on top of each histogram. Density of: **A**, *C. nicholsi;* **B**, *S. melanops;* **C** , *S. maliger;* **D**, *H. decagrammus;* **E**, *J. zonope;* **F**, *S. pinniger.*

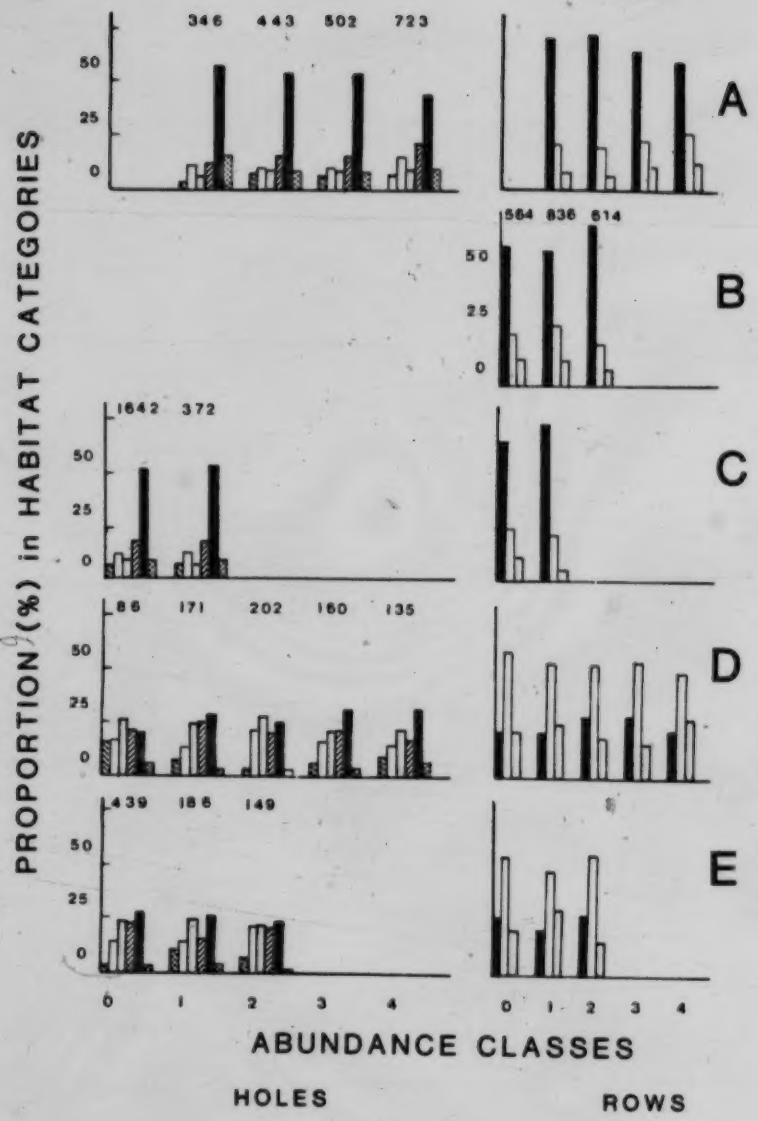

Figure 27: Effects of density of other species on the space utilization of *C. nicholsi* and *S. maliger* when a [DR] or [DH] interaction term was present in the fitted model. A–C: Space use of *C. nicholsi* against: A, *C. nicholsi;* B, *H. decagrammus;* C, *S. pinniger.* D–E: space use of *S. maliger* against: D, *C. nicholsi;* E, *J. zonope.* Legend as in Figure 26.

responses to its congeners were identical (increase of the use of the lower row and large holes, Fig. 26c and Fig. 26f). These shifts are not consistent with Pianka's (1972) hypothesis, as they increased overlap between *S. melanops* and its congeners: *S. maliger* used mostly the larger holes, and *S. pinniger* was most abundant on the lower row (Fig. 24). Similarly, its response to *J. zonope* produced greater overlap, since *S. melanops* increased its use of the upper row and larger holes (Fig. 26e).

S. maliger and *C. nicholsi* also responded to changes in density (Fig. 27), the former responding to benthic species (*C. nicholsi*, *J. zonope*, Fig. 27d, 27e) whereas the latter responded to *S. pinniger* and *H. decagrammus* (Fig. 27b, 27c). All four shifts were either erratic, or produced greater overlap between species. Only *C. nicholsi* and *S. melanops* broadened their own use of hole types, as their respective densities increased (Fig. 26a, Fig. 27a). These two species were also the only ones in which hole selection and row selection were associated ([RH] interaction term consistently present). Finally, *S. caurinus* and *H. decagrammus* did not show any shifts in their space use correlated to changes in the densities of other species. It must be noted however, that the changes that occurred were always small, not involving more than 20% of the populations.

C. Discussion

Although the reefs are totally artificial, they do provide a suitable environment for fish, measuring adequately their habitat requirements. Observations on the rock rubble slopes indicate that my microhabitat categorization of the reefs is representative of what exists in natural habitats (Chapter III). For instance, *C. nicholsi* is more commonly found on the lowest part of the rubble slope, where there is a mixture of small boulders and sand. It burrows underneath the rocks, as on the reefs, where it inhabits small holes in the lower section. The rockfish, on the other hand, are more abundant in the upper sections of the rock slope. The upper slopes are steeper, presenting larger areas of greater vertical relief than at the bottom of the slope. Rockfishes are often found hovering in narrow crevices alongside rocks, while on the reefs they also inhabit vertically oriented holes on the upper two sections.

It is difficult to define precisely what attracts fish to reefs (see Chapter IV), but it seems that the presence of shelter such as holes in the cement blocks, was crucial for most species. When disturbed or threatened by the divers, fish always retreated into holes, some (*C. nicholsi*, *J. zonope*, *Artedius spp.*) darting suddenly for cover, whereas the rockfish retreated more slowly. When disturbed, members of schools of *S. melanops* and *S. pinniger* usually did not retreat into holes, but remained in tight schools around the reefs. These schools never left the immediate vicinity of the reefs, but simply moved away from the divers while circling the structure. Only one species, *H. decagrammus*, did not seem to use the reefs as a refuge during daylight, but they did use them during night time (Chapter IV). When disturbed, they usually swam away and patrolled back and forth in the general vicinity of the reefs. *H. decagrammus* is apparently territorial (Leaman, 1980) and behaves as if using a reef as a central observation point and night-time refuge on their home site.

Two species made a more subtle use of space than this analysis indicates. As mentioned earlier (Chapter IV), *C. nicholsi* is associated with horizontal surfaces (ledges and sand bottom) and the great majority (> 80%) of the fish associated with a specific hole used the lower portion of the rows of blocks, nearest to the horizontal areas that they require. The association of *J. zonope* with vertical surfaces shows a greater degree of microhabitat specialization than is apparent with this analysis, and which is not entirely possible to quantify with the division of space in elevation and holes. The other species did not seem to make these fine distinctions.

The presence of interaction terms in the multidimensional contingency tables strongly implies that some interactions (either predatory or competitive in nature) are occurring. However, it must be noted that their correlative nature does not necessarily imply causal relationship. Nonetheless, correlative studies are probably the only possible approach in large community studies. Experimental manipulation of species abundance would certainly have provided more definitive answers. The artificial reef system was too small to manipulate the abundances in a single species pair (*S. caurinus-S. maliger*) successfully and obtain significant results (see Chapter VI). Manipulations that I have tried suggest that these two species did not

interact, as indicated by the contingency table analysis. In this system, with 8 common species, 28 sets of such experimental manipulations would have been required at the same time to test all possible combinations, an approach which is well beyond the capabilities of even the most enterprising experimenter. However, the results of this analysis will point out which of these pairs are most likely to interact.

The only uncontrolled variable in the contingency table analysis was the density of fish on the reefs. Three factors created by the experimental design could have affected the pooling of density into classes, (1) time of year, (2) the replicate (i.e. reef no.), and (3) the species present on the reefs. The density classes were independent of season, as most of the species showed little seasonal fluctuations in abundance; the two exceptions (*S. melanops* and *S. pinniger*) were noticeably more common in summer. I have shown in Chapter IV that the assemblages present on each of the reefs were independent of the position of the replicates. I have also shown that the abundance of pairs of species were never correlated over the reefs, indicating that the abundance of a given species was totally independent of the abundance of other species.[2] Thus, in spite that communities inhabiting the reefs were not entirely homogeneous (Chapter IV), there is no evidence that these differences were correlated to any of the factors of interest (i.e. replicate, time of year, or species present). As a matter of fact, this analysis could not had been performed if the communities on the reefs had been entirely homogeneous, since it is based on the assumption that some differences existed between them.

The mean number of fish per species was small (< 5) and thus even small changes in absolute abundance created large proportional differences. These changes were probably the results of "random" fluctuations. They were not related by any means to the three factors (seasons, with 2 exceptions, species present, and replicate) resulting from the pooling of the data. The assemblages present on these reefs are the result of colonization by fish coming from the rock rubble slope; reef isolation had only minimal effects on density (per unit area) and species composition

[2] Correlations were calculated between the abundance of the 8 commonest species on the reefs (28 pairs), yielding 1512 correlations (28 pairs x 54 censuses) for the insular reefs and 756 correlations (28 pairs x 27 censuses) on the continental reefs. Only two of these were significant ($p < 0.05$, 1 negative, 1 positive), both on the insular reefs.

(Chapter IV). Colonization on isolated, "insular" habitats appears to be primarily a stochastic process (MacArthur and Wilson, 1967) which is likely to produce random fluctuations in abundance. In Chapter VI, I will show, using a randomization test (Sokal and Rohlf, 1969), that the assemblages found on these reefs cannot be distinguished from what would be expected from a purely stochastic colonization process. The use of this natural variability is thus quite reasonable, and the density effects of the Chi-square are most certainly dependent upon changes in fish abundance, and not on some other factor correlated to abundance.

Because of the numerous models tested, a large number of significant terms would have been produced by type I error. The use of the 1% probability level, instead of the traditional 5%, minimized this (Whittaker and Aitkin, 1978). Only 2 interactions terms involving density, which would have been accepted at 5%, were rejected at the 1% level (1: *C. nicholsi vs.*, *S. melanops*, [HD,HR], X^2 = 61.26, df = 40; 2: *S. maliger vs. H. decagrammus*, [DH,R], X^2 = 39.64, df=34) However, the indicated shifts were either without patterns (1) or resulted in greater overlap (2).

Habitat shifts occur frequently in terrestrial communities, and they have usually been attributed to interspecific competition (Schoener, 1970; Diamond, 1978). For fish communities, Werner and Hall (1976), Hixon (1980) and Larson (1980a) have all experimentally demonstrated that with release of competitive pressure, members of pairs of congeners increased their habitat use. Concentrating on habitat is expected to be the most likely approach for detecting competitive effects. Habitat shifts are not necessarily the result of spatial competition between territorial species; Werner and Hall (1976) have shown that food competition in artificial assemblages of sunfish (*Lepomis spp.*) resulted in marked shifts in habitat use. In this case, space itself appears to be important. Two benthic species (*C. nicholsi*, *H. decagrammus*) are territorial (Leaman, 1980; K.S. Cole, personal communication) and the remaining two (*J. zonope*, *Artedius spp.*) are presumed to be so. Agonistic encounters between *J. zonope* (or *Artedius spp.*) individuals were commonly seen on the reefs, even more frequently than between individuals of the two species which were known to be territorial.

The study has revealed a much smaller number of significant interaction terms involving density than I would have predicted from the studies mentioned above. Furthermore, most of the interaction terms appear to be occurring between groups (eg. rockfish vs benthic species) rather than within groups of closely related or ecologically similar species.

Only two shifts appear to have reduced effective overlap between species (*S. melanops* vs. the benthic species, *C. nicholsi*, and *H. decagrammus*), suggesting possible competitive interactions resulting in greater niche separation. Thus, *S. melanops* was the only species to behave in a way compatible with an interpretation based on competition. *S. melanops* belongs to a group of midwater *Sebastes* (Hallacher, 1974), and according to my observations only occasionally takes refuge in crevices. Even then, it is probably associated only marginally with the reefs, being more susceptible to interference by other species which did associate closely with the substrate. It is not surprising that the demersal species affect *S. melanops* as they are (or are presumed to be) all territorial (K.S. Cole, personal communication; Leaman, 1980), thus having a profound effect on space availability.

C. nicholsi and *S. melanops* were the only two species that broadened their spatial distribution as they became more abundant on the reefs. These two interactions indicate that intraspecific pressure affected their space use. These two species were by far the most common and probably the only ones to reach densities high enough to produce interactions, some fish being forced out to less favourable (?) habitats.

On the other hand, the remaining significant shifts actually increased overlap, and they cannot be easily attributed to niche separation. When the density of benthic species increased, *S. maliger* shifted towards the kinds of microhabitat that these benthic species used (eg. increase in overlap with *C. nicholsi* and *J. zonope*). Similar shifts occurred in other species: *C. nicholsi* vs. *S. pinniger*, and *S. melanops* vs. *S. pinniger* and *J. zonope*. These results are not consistent with the prediction of Pianka's (1972) "niche overlap hypothesis". More importantly, these results differ from experimental works that demonstrated competition (eg. Werner and Hall, 1976; Hixon, 1980; Larson, 1980a). They probably indicate that some other factors are operating

(eg. predation) but these are not readily identifiable, on the basis of the present information. For example, the larger rockfishes (eg. *S. maliger*) may be preying on the smaller demersal species (eg. *C. nicholsi, J. zonope*), following them into their habitat, thus effectively increasing overlap. Mutualistic interactions would tend also to increase overlap. However, there is no published experimental work which would allow me to make such interpretations, and these must remain purely speculative at this stage.

In conclusion, nine interactions between species, which affected their space utilization, were detected. Two of these (*S. melanops vs. C. nicholsi* and *H. decagrammus*) can be reasonably interpreted as being the result of interspecific competition, an interpretation based on the results of previously published empirical studies (eg. Werner and Hall, 1976; Hixon, 1980; Larson, 1980a). The seven other interspecific interactions are more puzzling! The original 28 possible pairs of potentially interacting species has been reduced by almost 60%, through this analysis, and experimental work is needed to discover the biological basis of these interactions.

I had expected many more interactions between these species, especially among members of ecologically similar species. The rationale behind the removal experiment involving *Sebastes caurinus* and *S. maliger* (to be described in the next chapter) was based on the close similarity of their habitat requirements, which had led me to postulate that they should strongly interact. The causes for the absence of interactions are as yet unknown, and more work is needed in this field. It may be a consequence of the generally low density of these fish on the reefs, which may be too low for the interactions to have significant effects on the spatial distribution of fish. It is noticeable that the only two species that showed density dependent control of their space use (*C. nicholsi* and *S. melanops*) were the most common and affected most the spatial distribution of other species, or were affected the most in their spatial distribution. In the next chapter, I examine the importance of these interactions on the development and the structure (i.e. the presence and abundance of species) of the reef fish communities.

VI. RESULTS IV and GENERAL DISCUSSION:

Determinants of community structure

The recent controversy on fish community structure (Sale, 1980b; Anderson *et al.*, 1981) has focused on the respective roles of deterministic factors (eg interspecific competition) and stochastic events as the principal determinant of community structure. The main sources of evidence that have served to fuel this controversy have been chiefly distributional studies on isolated reef patches, that were usually experimentally established (i.e. artificial reefs) (Sale and Dybdahl, 1975, 1978; Talbot *et al.*, 1978; Bohnsack and Talbot, 1980; Gladfelter *et al.*, 1980). The area of contention has been whether these communities are approaching an equilibrium (mediated through interspecific competition) or not. The equilibrium state was considered reached when a series of communities inhabiting identical habitats developed toward a common equilibrial state (using some indices of community similarity). The equilibrial conditions, and the level at which one accepts that communities are in fact at equilibrium, usually remain undefined and the debate has centered on whether communities appear sufficiently similar to be in equilibrium or not (Talbot *et al.*, 1978; Gladfelter *et al.*, 1980). Finally, the effects of patch size have been neglected in the interpretation of the results. Sale (1980b) has argued – based on the central limit theorem – that estimates of community similarity are strongly dependent on the size of the area sampled; the larger the area, the more similar communities will be, regardless of the mechanisms involved.

The purpose of this chapter is to examine in detail these two points, and to determine objectively if community patterns diverge from those expected under the non-equilibrial conditions. In order to test the effects of patch size, two additional sets of reefs were built in 1980: (1) the new insulars (serving as temporal controls) and (2) the small reefs (testing the area effects).

A. Analytical approach

Theoretical considerations

The colonization of small isolated reefs can be viewed, at least initially, as being a purely stochastic process, the colonists arriving at random from the surrounding rocky habitats on these newly created patches. As the reefs reached a species equilibrium[3] (from 13 to 25 weeks in this study), the communities on each of these isolated patches would enter an assortative phase (Wilson, 1969) resulting in communities moving toward C-equilibrium, assuming of course that additional regulatory processes are involved in controlling the composition of the community.

Interspecific competition is the process which is usually assumed to produce C-equilibrial conditions (Anderson *et al.*, 1981). These C-equilibrial conditions will be ultimately determined by the resources available on these habitat patches and by the niche parameters of the species present. Since all the artificial reefs were identical, the C-equilibrial conditions on all of them should be the same; in perfectly deterministic conditions, the fish assemblages inhabiting each and every one of these units should be exactly similar (community difference = 0%). One should then observe that communities inhabiting such units will be significantly more similar to each other than communities produced by purely random colonization (S-equilibrial communities in the pre-assortative phase), if interspecific competition plays a significant role in this system by bringing the communities at or near C-equilibrial conditions. Therefore, the proper null hypothesis for such a test is that the communities on these reefs are simply the results of random colonization from the surrounding habitats.

Simberloff (1978) has extensively discussed these problems, and he proposed techniques to determine whether or not the colonization of islands is stochastic. He proposed two additional, non-interactive hyptheses, which may account for the distribution of species on islands (or isolated patches).

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[3] There is an unfortunate double used of the unqualified term *equilibrium* in the ecological literature, both of which are relevant to this study.

1. Species-equilibrium (MacArthur and Wilson, 1967) is the equilibrium between immigration and extinction rates in the number of species present on island. I shall call it here *S-equilibrium*.
2. Community equilibrium (Connell, 1978), which is the stable specific composition attained by a community. This stable condition is mediated through interspecific competion, and following a disturbance, the community will be driven back to that equilibrium by competion. It is denoted here as *C-equilibrium*.

1. Small island limitations: diversity of habitat types on a small island is usually less than on a large island or the mainland. Species adapted to the absent habitats may be absent on these smaller islands, thus effectively reducing the pool of available colonists. More generally, the different patches will usually differ in the quality of the habitat, and different subsets of species adapted to different habitats may be found on different patches. In this case, the habitat created by cement blocks is structurally quite different from the rock rubble, and different subsets of species should be expected in these two habitats. This first limitation is more generally renamed habitat availability constraint.
2. Weighted colonization probabilities: The colonizing abilities of the different members of the community are likely to differ, and a barrier (10 m of sand for example) which may appear unsurmountable for one species may be readily crossed by another, thus also affecting greatly the pool of species available for colonization of such units. These are called distance constraints.

Earlier work (Connor and Simberloff, 1979; Simberloff and Connor, 1981) have been marred by a lack of independent estimates of these two additional factors, requiring that they be estimated from the original data. In this case, I have independent estimates of these two additional parameters, allowing me to formulate 3 further hypotheses.

1. Hypothesis I: Random settlement from the rock rubble slope. This is the model without constraints, and the data collected on the transect can be used as an estimator of the species pool available for colonization.
2. Hypothesis II: Random settlement with the habitat availability constraints. The community composition of the continental reefs, which are structurally similar to the insular reefs, but which are in direct contact with the rock rubble (no distance constraints), can be taken as an estimator of a typical mainland species pool inhabiting artificial structures.
3. Hypothesis III: Distance constraints. The difference between insular reefs and continental reefs can be taken as an estimator of the distance effects, as only distance between the two differed. However this estimate is not independent of the community under investigation. Independent communities were provided by

the small insular reefs, which have the same structural appearance and which are at the same distance from the rock rubble than the insular reefs. Only size, which may affect the S-equilibrial conditions was different, the small reefs being one third of the size of the original insular reefs.

Analytical procedure

In order to determine whether the assemblages of fish present on the reefs did differ significantly from the assemblages resulting from purely stochastic colonization events, a randomization test (Sokal and Rohlf, 1969:629) was performed. The randomized statistics were the mean community difference on a series of 6 artificial reefs. In order to estimate community difference, an overlap index was used. The index selected was percent difference, recommended by Goodall (1978) as showing less sample size dependent biases. Percent difference is given by:

$$PD = \frac{\sum_{i=1}^{S} |Xij - Xik|}{\sum_{i=1}^{S} |Xij + Xik|}$$

where Xij and Xik are the number of species i in sample j and k respectively (see Chapter IV).

Six random communities were generated by drawing at random, using a pseudo-random generator, individual fish from the species pool and calculating the mean percent difference between all pairwise comparisons. Five hundred of these sets of random communities were generated to produce an expected distribution of the statistic. The number of fish randomly assembled on these simulated reefs was drawn at random from a distribution with the same mean and variance as that observed on the natural reefs (mean = 19.2 fish/reef, variance = 59.07), preliminary randomization runs having indicated that these two variables had a considerable influence on the statistic.

The hypothesis tested is that the communities on these entities have undergone an assortative phase under the influence of interspecific competition, that is they are approaching C-equilibrium (percent difference tending toward 0.0%). The null

hypothesis for the test is that the communities are solely the result of the initial colonization process (percent difference not different from random expectation). This is then a one-tailed test, the lowest 5% generated values of mean community difference forming the region of rejection for the null hypothesis.

B. Results

Colonization history of the small and new insular reefs

The colonization of the small and new insular reefs was essentially identical to that of the previous three series. Seventeen (15 residents) were recorded on the small reefs whereas 12 species (all residents) were recorded on the new insular reefs (Table 5). The same species were present on these 2 new series of reefs. Colonization rates for these 2 series are plotted in Figure 28. By comparing these colonization curves to those obtained on the two original series of insular reefs (Fig. 11), it appears that the small reef had reached the S-equilibrium level in 18 weeks. The last 5 censuses showed a mean no. species/reef > 4. In order to determine if S-equilibrium had been reached, I used a similar criterion as earlier (see Chapter IV), but with a lower level (4 species instead of 5) to compensate for the smaller area. The new insular reefs had reached the S-equilibrial level (5 species/reef) of the old insular reefs (Fig. 11) in 19 weeks. These levels and the period required to attain them are similar to those observed on the original series of reefs, and we may assume that these series were then truly at S-equilibrium. The mean number of fish per reef reached similar levels on the new series as on the old ones. At S-equilibrium, the new insulars had a mean of 22-25 fish/reef, a value equal or slightly greater than on the 2-year old reefs, whereas the mean number of fish varied around 7 on the small reefs, nearly one third of the value observed on the large reefs which were three times as large.

Removal experiment

Thirteen fish (4 *Sebastes caurinus* and 9 *S. maliger*) were removed in reciprocal experiments from reefs 3, 4, and 5. The results are presented in Table 12. Because of the small size of the populations inhabiting the reefs, the sample sizes are very small, making reliable statistical testing impossible. It appears that the eliminated

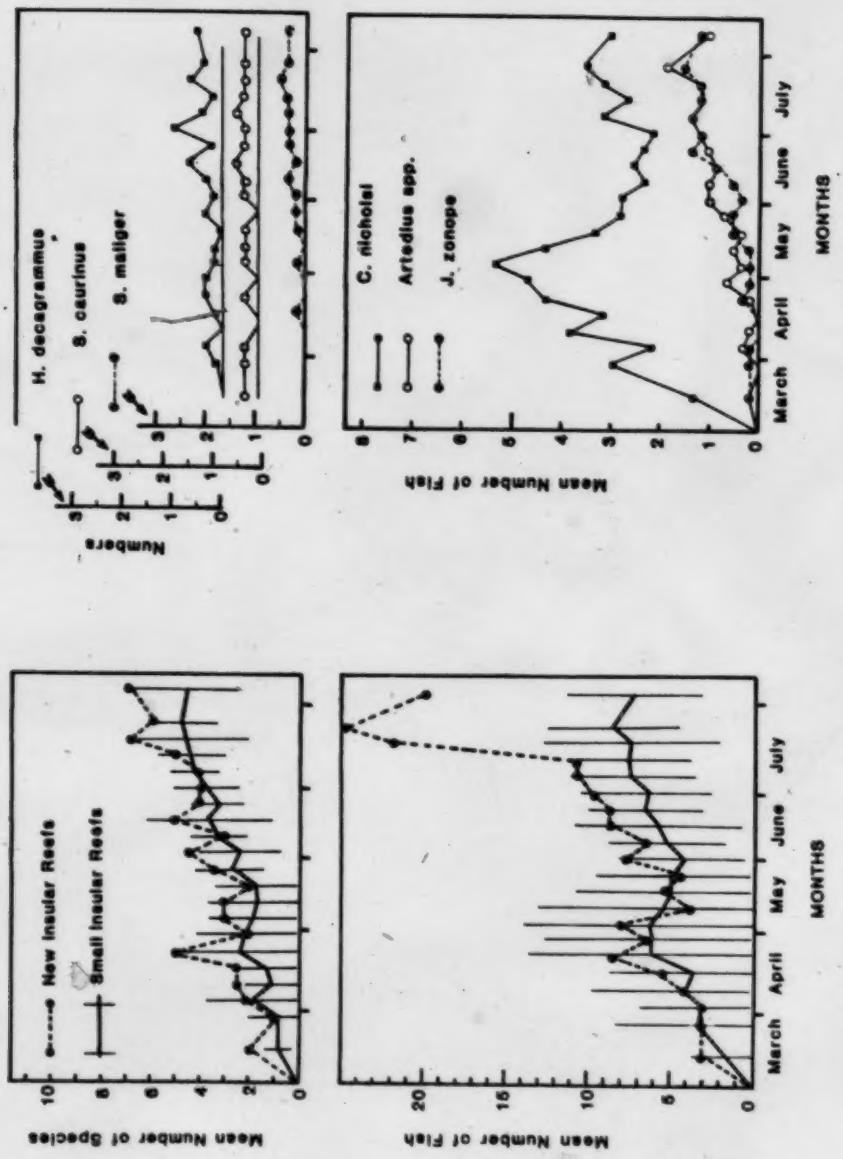

Figure 28: Colonization history of the small and new insular reefs. The vertical bars indicate the 95% confidence intervals.

Table 12: Results of the removal experiment:

Experiment:	Reef	Numbers before 6/5/1980		Number removed 10-16/5/1980		Numbers after 3/6/1980	
		SC[1]	SM[2]	SC	SM	SC	SM
Control	2	0	3	0	0	1	6
Control	6	1	5	0	0	4	4
Sebastes caurinus removal	5	1	3	2	0	4	4
Sebastes maliger removal	4	1	4	0	8	2	8
Both species removal	3	1	1	2	1	2	1

1. SC = *Sebastes caurinus*
2. SM = *Sebastes maliger*

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species reinvaded the reefs in numbers approximately similar to the number removed (9 *S. maliger*, 6 *S. caurinus*), whereas the other species never greatly increased as a result of the removal. Unfortunately, the controls (reef 2 and 6) showed as much variation as the experimental reefs, rendering the experiment inconclusive. This approach is usually useful in providing clear evidence of interspecific competition. Its failure here is a result of logistic problems, the artificial reef system being much too small to perform it satisfactorily. Massive removals would be required, and they cannot be performed inside this system.

Community structure

The frequency distributions of the randomly generated index, under the three sets of assumptions are presented in Figure 29. The distributions shift to the right as the number of constraints (habitat availability and distance) are added to the model. The mean and critical values of these distribution are presented in Table 13. The shifts to the right of the distributions, indicating an increase in dissimilarity in community composition, are the result of an increase in diversity on the insular reefs in relation to the transects and the continental reefs. For instance, *Coryphopterus nicholsi*, the most abundant species in this system represents more than 87% of the sightings on the transects, 62.1% on the continental reefs and only 40% on the insular reefs. This increases the probability that species other than *C. nicholsi* will be drawn in the simulations (thus increasing dissimilarity) as the number of constraints is increased.

Because the successive series of observations were not independent, the observed distribution of the mean percent differences between the reefs could not be compared directly to the random distributions, using a goodness of fit test (eg. Gatz, 1979). Visual observation of the distributions reveals immediately that strong divergence occurred between the observed distribution, the random distribution (of hypothesis I) and the random distribution with habitat availability constraints (hypothesis II). The observed distribution showed only small divergence with the distribution modified by both constraints (habitat availability and distance, hypothesis III). In this case, as in all further tests, the first 4 months of colonization were not included (10 first surveys) since the reefs had not yet reached S-equilibrium. It then appears that

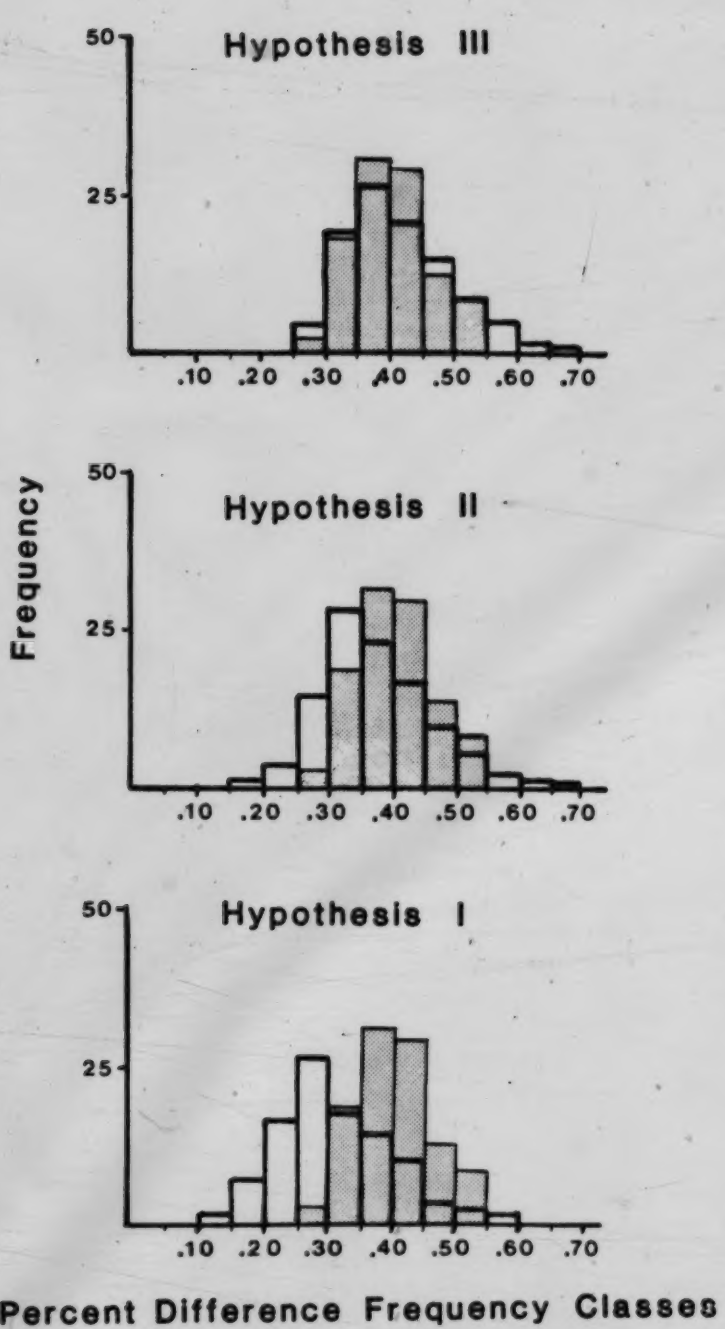

Figure 29: Generated distribution of the mean percent difference under 3 sets of assumptions, with a comparison with the observed values. Grey bars: observed values; white bars: generated values. Hypothesis I: random colonization. Hypothesis II: random + habitat constraints. Hypothesis III: random + habitat and distance constraints.

Table 13: Critical values of the null distributions under different sets of assumptions based on 500 simulations.

Model	Species pool	Mean Percent difference (Variance)	Lower 95% confidence limit
Random colonization.	Transects.	0.3148 (0.03456)	0.1883
Random colonization, with habitat constraints.	Continental reefs.	0.3743 (0.02742)	0.2527
Random colonization, with habitat and distance constraints. Mean community size: 19.4 fish (large reefs).	Insular reefs.	0.4119 0.02514)	0.3011
Random colonization, with habitat and distance constraints. Mean community size: 7.4 fish (small reefs).	Insular reefs.	0.5385 (0.03608)	0.3952

without the two constraints, random colonization is a poor predictor of community composition.

In order to detect significant divergences between the observed values of mean community difference and the three generated distributions, each of the successive observed values were checked against the 95% confidence limits; any value falling below the 95% confidence limits were considered to be significantly different from values belonging to the random distributions (Sokal and Rohlf, 1969:629), indicating that the communities were more similar than they would be through random settlement from the rock rubble (with the added constraints). They would be then considered to be approaching C-equilibrial conditions.

In addition to avoid the problems of dependence, this approach also allows the detection of seasonal trends; there is no *a priori* reason to suppose that conditions will remain constant throughout the year (see Chapter IV), and that interspecific competition may be important at the period of peak abundance (summer) whereas it may be less important in winter at period of lower abundance.

Temporal fluctuations in the mean percent difference between the reef communities are plotted in Figure 30. Discarding week 1 to 20 as previously (before S-equilibrium was reached), it can be seen that no values ever fell below the 95% confidence limits of distribution I and II (random, and random + habitat availability constraints). These 2 distributions are, for theoretical reasons, poor predictors of community development and these results probably do not have much significance. Only one point (sampling period no. 53, 27 July 1980, **PC** = 0.293) did fall below the 95% confidence limit of distribution III (random colonization + both constraints), indicating that the communities were at that period significantly more similar to each other than expected by chance alone (Table 14). Because of the large number of tests (44), one significant value can be expected from type I error, and there is no ground on these results to reject the null hypothesis that the community composition on these reefs is uniquely the result of random colonization.

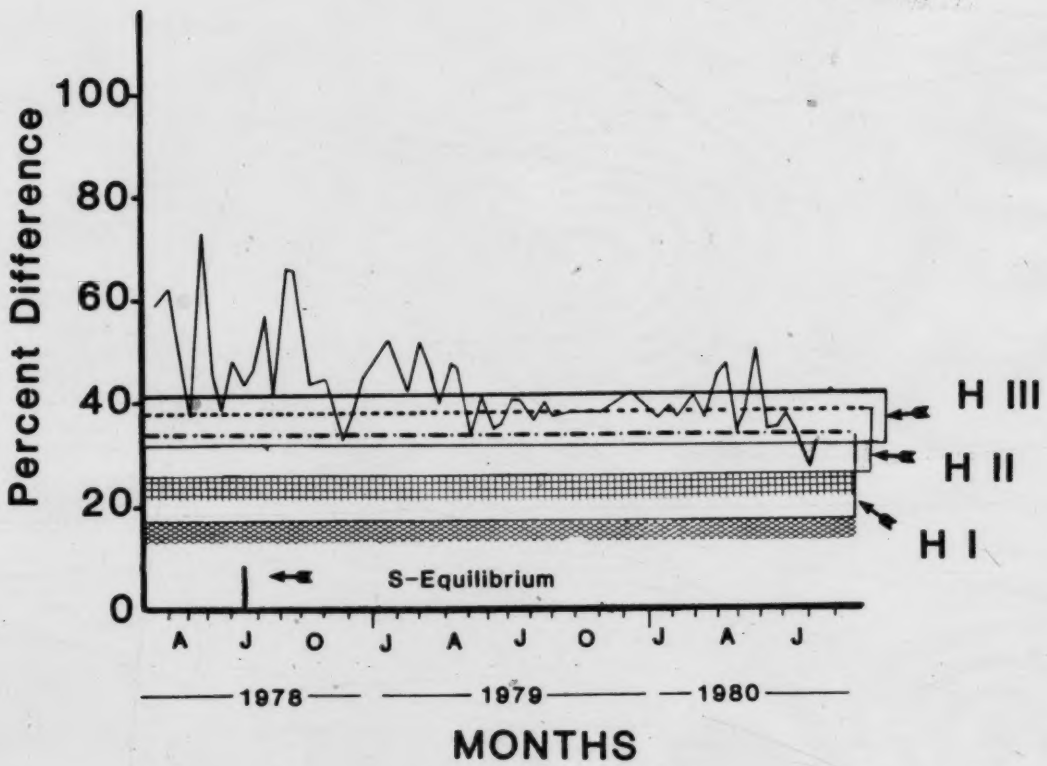

Figure 30: Temporal fluctuation in percent difference between the reef communities. The critical values of the generated distributions (H I, H II, H III) are indicated. Heavy lines: mean of the distributions. Upper edge of the connected shaded zones: lower 95% confidence limits. S-equilibrium was determined from the colonization record (Fig. 11).

Table 14: Mean percent different values between the reefs and their percentiles in the null distribution (Hypothesis III)

Survey	Insular reefs			Small reefs		
	Mean[1]	N[2]	Perc.[3]	Mean	N	Perc.
	Pre S-Equilibrium values					
1	0.584	6	0.969			
2	0.621	6	0.989			
3	0.467	6	0.759			
4	0.375	6	0.368			
5	0.730	6	1.000			
6	0.451	6	0.712			
7	0.377	6	0.382			
8	0.489	6	0.827			
9	0.436	6	0.654			
10	0.463	6	0.748			
	Post S-Equilibrium values					
11	0.561	6	0.946			
12	0.407	6	0.532			
13	0.659	15	0.997			
14	0.652	10	0.996			
15	0.429	15	0.625			
16	0.443	15	0.682			
17	0.324	10	0.137			
18	0.374	15	0.362			
19	0.447	15	0.696			
20	0.530	15	0.905			
21	0.411	15	0.551			
22	0.518	15	0.886			
23	0.478	15	0.794			
24	0.410	15	0.544			
25	0.477	15	0.790			
26	0.478	15	0.792			
27	0.336	15	0.183			
28	0.429	15	0.622			
29	0.343	15	0.209			
30	0.360	15	0.288			
31	0.421	15	0.591			
32	0.403	15	0.518			
33	0.365	15	0.318			
34	0.418	15	0.580			
35	0.371	15	0.347			
36	0.387	15	0.436			
37	0.387	15	0.434			
38	0.426	10	0.612			
39	0.375	15	0.371			
40	0.404	15	0.522			
41	0.376	15	0.377			
42	0.421	6	0.591			

Table 14: continued.

Survey	Insular reefs			Small reefs		
	Mean[1]	N[2]	Perc.[3]	Mean	N	Perc.
				Pre S-Equilibrium values		
43	0.372	6	0.356	0.744	15	0.984
44	0.458	10	0.733	0.826	15	0.998
45	0.490	10	0.828	0.812	15	0.997
46	0.342	10	0.205	0.793	15	0.995
47	0.397	10	0.486	0.780	15	0.993
48	0.514	10	0.880	0.783	15	0.993
				Post S-Equilibrium values		
49	0.349	10	0.233	0.762	15	0.990
50	0.356	10	0.271	0.661	15	0.899
51	0.384	10	0.420	0.587	15	0.718
52	0.340	10	0.200	0.552	15	0.585
53	0.293	10	0.040	0.482	15	0.283
54	0.332	10	0.169	0.555	15	0.594

1. Mean percent differences between all pairs of reefs.
2. Number of pairwise comparisons.
3. Percentile of the generated distribution for the observed value (i.e. area under the distribution curve with generated values smaller than the observed value).

Randomization of the small reef communities

One might argue that since the species pool from which random settlement with both the habitat availability and distance constraints was generated was not independent of the experimental values, the lack of demonstrable differences being merely the result of this lack of independence. The small reefs provide an experimental community which is independent of the species pool used for generating the randomized distributions (insular reefs). Further, it is subject to the same colonization constraints than the insular reefs, the only diference being the mean number (and variance) of fish per reef (mean = 7.2; s^2 = 9.3). Finally, they had been in existence for a sufficiently long time to assume that they had reached S-equilibrium. The random communities were generated exactly as before, using the new values for community size. The distribution of the index is given in Figure 3.1, whereas the temporal fluctuations in the mean community difference between the small reefs are plotted in Figure 32, against the critical values of the generated distribution. Again, discarding the first 20 weeks (before S-equilibrium), it can be noted that none of the remaining values ever fell below the 95% confidence limits (Table 14), confirming the conclusion reached previously.

C. Discussion

The patterns of fish community composition on the artificial reefs do not give any indications that interspecific competition had any role in determining the specific composition and the relative abundance of species (i.e. community structure) on the artificial reefs. The null hypothesis, that communities are essentially the result of random colonization (given 2 additional constraints: that distance affects colonization, and that habitat affects community composition), could not be rejected on the basis of the colonization patterns.

An alternative hypothesis, easily dismissed, is that the reef communities were not truly independent from each other, rendering meaningless community interpretation based on distributional patterns at the patch level. The tagging results (Chapter IV) clearly contradict this possibility. All the tagged fish remained continuously on the reefs for long periods (many months) and were not free-ranging on the study site, as

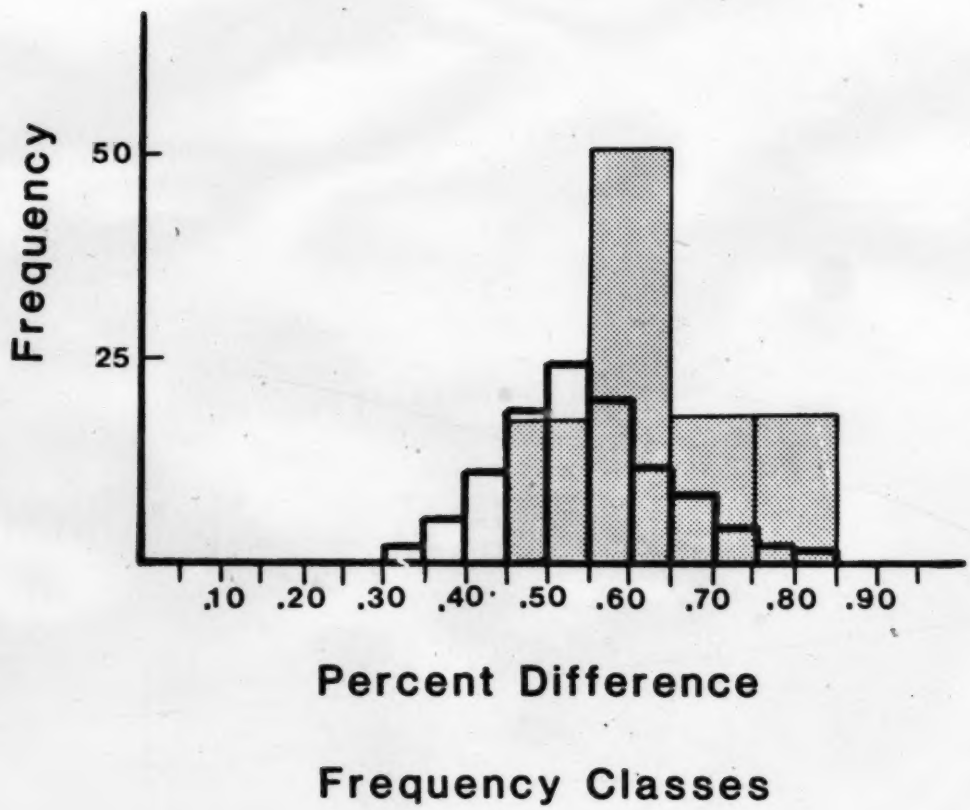

Figure 31: Generated distribution of the mean percent difference between small insular reefs with habitat and distance constraints. Grey bars: observed distribution based on the 6 points following S-equilibrium. White bars generated values.

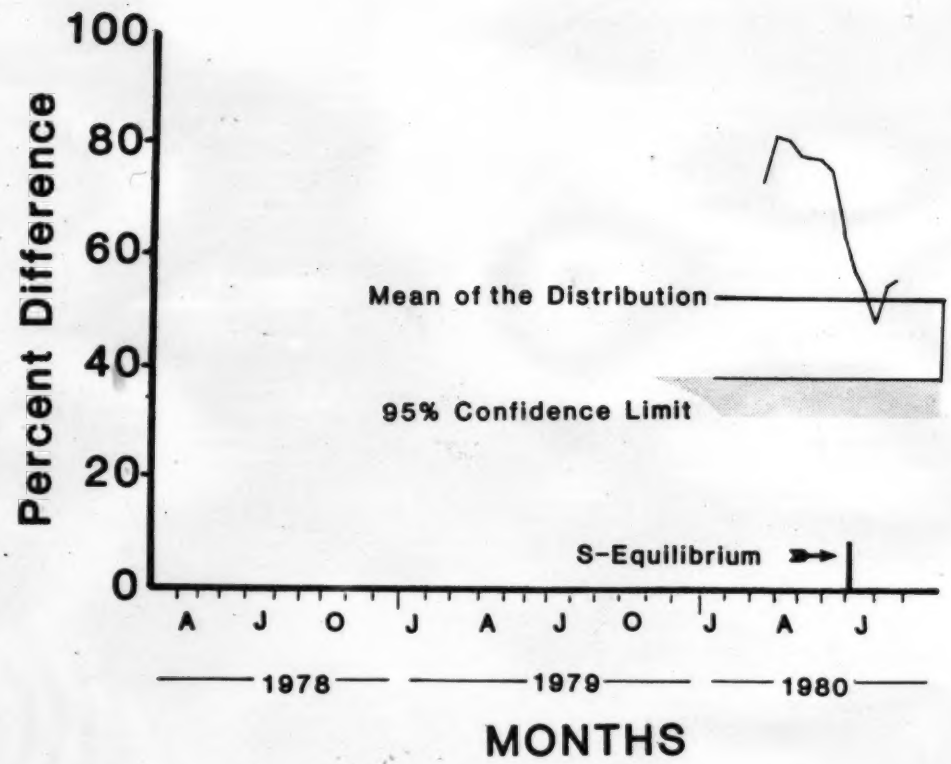

Figure 32: Temporal fluctuation in percent difference between the small insular reef communities. The critical values of the generated distribution (with distance and habitat constraints) are indicated as in Fig. 30.

none of the tagged fish were seen on reefs other than the one on which they were tagged. Published results also concur (Carlson and Haight, 1972; Dewees and Gotshall, 1974; Love, 1979; Leaman, 1980; K.S. Cole, personal communication), all the species in question having been described as territorial or with restricted home ranges. Thus, the distributional patterns on these independent patches should reflect the influence (or lack of) of the species interactions on community structure, as these interactions will be limited mostly to the immediate vicinity of each independent patch. Under these circumstances, the distributional patterns cannot be merely a temporary assembly of free ranging fish that happened to be on a given reef at the time of the sampling.

The reef communities had reached a species-equilibrium rapidly (within 6 months). This S-equilibrium was dynamic, as both species and individual fish emigrated or immigrated continuously (Chapter IV). This analogy of marine benthic patches with insular systems has led to some interpretations based on the theory of island biogeography (eg. Schoener, 1974a, 1974b; Molles, 1978; Osman, 1978; Bohnsack, 1979). In these patchy marine environments, the patch's carrying capacity appears to be a stronger determinant of community size than species equilibrium number. As opposed to oceanic islands, for which the theory of island biogeography was specifically developed (MacArthur and Wilson, 1967), the patch population sizes are not the result of intrapatch demographic processes, but of immigration (or emigration) by individual fishes. Many of the species were present in the non-reproductive phase of their life cycle (eg *Sebastes spp.*) or produced highly dispersive planktonic larvae. The S-equilibrial conditions are a simple statistical consequence of having a determined number of propagules (i.e. the number of fish per reef) coming from a given species pool. On the other hand, on oceanic islands the population sizes are relatively independent of immigration rates and species emigration (or extinction), and thus the species numbers become biologically meaningful (Smith, 1975). See Gilbert (1980) for a thorough critique of these studies on island biogeography. In this study, the S-equilibrium itself was not considered, as all the randomizations were done on the basis of a fixed carrying capacity (mean no. fish/reef of 19.2, with a variance of 59.07); the S-equilibrial conditions were observed to develop in the test as a result

of the randomization procedure. The S-equilibrium is nevertheless convenient and may be used to indicate that no further directional changes were taking place in the communities. The lack of an assortative phase in community development, as indicated by the randomization tests, cannot therefore be attributed to unsaturated communities under active colonization where interactions are unlikely to occur.

Clearly, the simple measure of community similarity cannot be held as strong evidence for determinants of community structure. The Barkley Sound communities were remarkably similar in their species composition (around 60%, see Chapter IV), a result very different of that found by Talbot *et al.* (1978) who reported values of 30-35% for coral reef fishes on structures essentially similar to those used here. They interpreted these low similarity values as a strong indication of the non-equilibrial conditions of their system. On the other hand, Gladfelter *et al.* (1980) interpreted the high degree of correlation between measures of community similarity and measure of habitat similarity (and the consequent high similarity between the communities inhabiting similar environment) as an indication that the coral reef communities that they were studying were in equilibrium, precise sets of co-adapted species being present in each type of habitat.

Even if the Barkley Sound communities are more predictable than tropical systems (Chapter IV) and develop apparent equilibrial conditions (according to the above criteria), the randomization showed that none of the postulated mechanisms (i.e. interspecific competition) of the equilibrial conditions were at work. Many variables appear to affect the neutral values (i.e. under purely random conditions) of community similarity: population size (Sale, 1980b), its variance (see above), and most probably species diversity. A reduction in one component of diversity (evenness) [as communities were generated using different species pools: insular reefs, continental reefs, transects] produced an increase in neutral community similarity (from 60% to 70%); the second component of diversity (no. of species) has presumably a similar effect. Since in all previous studies (Sale and Dybdahl, 1975; Gunderman and Popper, 1975; Talbot *et al.*, 1978; Brock *et al.*, 1979; Gladfelter *et al.*, 1980; Anderson *et al.*, 1981; Ogden and Ebersole, 1981) these parameters differed, it is impossible to assess the biological meaning of the reported patterns of community similarity.

Simberloff (1978), Lawlor (1980a, 1980b), and Strong (1980), faced with similar problems, have stressed the importance of formulating the proper null hypothesis when investigating patterns at the community level. Neutral models (Caswell, 1976) have been usually used to generate the numerical values of the null hypothesis, by producing community patterns in the absence of the factor of interest (usually interspecific competition) to which actual communities may be compared. These models have been built to test distributional hypotheses (Pielou, 1977, 1978; Simberloff, 1978; Connor and Simberloff, 1979; Simberloff and Connor, 1981) and to test hypotheses on the evolution of niche parameters (Sale, 1974a, Caswell, 1976; Gatz, 1979; Strong *et al.*, 1979; Joern and Lawlor, 1980; Simberloff and Boecklen, 1981). Both types have been plagued so far by problems of statistical significance and of independence (between the data set used to generate the hypothesis and that used to test it) (Grant and Abbott, 1980; Lawlor, 1980a, 1980b; Hendrickson, 1981; Diamond and Gilpin, 1982).

Connor and Simberloff (1979) and Simberloff and Connor (1981) have re-examined claims of competitive exclusion based on distributional patterns on islands by formulating what they claimed to be the proper null hypotheses (that is in which the factor of interest – in this case competition – does not intervene). Additional important biological parameters (eg. distance and habitat effects [Simberloff, 1978]) might have affected the distributional patterns independently of competition in the studies that they re-examined. They estimated these factors directly from the original data sets, according to precise criteria. These *a posteriori* manipulations create interpretational problems. Without proper controls, it is impossible to distinguish the effects of these factors from those of competition. Their manipulations of the data sets may have eliminated all factors (both the dispersal constraints, that they were attempting to control, and the competitive effects), rendering their results trivial (Diamond and Gilpin, 1982).

Gilpin and Diamond (1982) and Wright and Biehl (1982) have recently proposed analytical methods to estimate the probabilty of species co-occurrence on islands. Their approach removed some of the statistical problems present in the Monte Carlo technique used by Connor and Simberloff (1979) to estimate the co-occurrence

probabilities of species. However, these analytical methods are not any better at solving the additional problems inherent to this kind of study (that of independence and those associated with additional biological constraints, such as distance and habitat effects), which result from the uncontrolled nature of the data. Their approach, which emphasizes patterns of co-occurrence of species, could not have been used here because, as I argued earlier, the reef patches are not true insular systems on which the patterns of species presence-absence are biologically meaningful.

The experimental design, using artificial reefs, controls these additional constraints. The effect of these variables can be independently estimated, removing the weaknesses of the previously described re-interpretations. Although the randomization of the insular reefs did not have a control for distance, the randomization of the small insular reefs did (insular reefs), making this test entirely controlled. The exclusion of these additional factors (distance and habitat effects) would not have altered the conclusions (acceptance of the null hypothesis) although it would have certainly made the test less plausible and excessively conservative, a result of the greater evenness in the insular communities. This was an unpredicted phenomenon, an apparent consequence of the poor dispersal of the most abundant species, *Coryphopterus nicholsi*.

The lack of demonstrable effects of competition on the structure (i.e. the number of species and their relative abundance) of the reef fish community does not indicate that it is not present, but that it has no effects at the community level (level II). The results of the previous section (Chapter V) indicates that competition at the species level (level I), at least on the spatial dimension does not exist, even though it is the most likely (Schoener, 1974; Sale, 1980b). That precludes interspecific competition from having any effects at the community level. Strong competition might be detected in another, uninvestigated dimension (eg. food), still requiring the consideration of an hypothesis at a higher level. These are in fact two different problems, which are not always distinguished in the literature, and depending on the level (species or communities) at which the phenomena are examined, different answers might be found.

When competition results in exclusion (Hixon, 1980; Larson, 1980a, 1980b, for marine fishes; and for example Reynoldson and Bellamy, 1971; Heller, 1971; Hairston, 1980, for other group of organisms), the two questions become one, as the presence and abundance of species are clearly determined by competition. On the other hand, when competition is of a more exploitative nature (Brown and Davidson, 1977; Inouye, 1978; Brown *et al.*, 1979; Davidson *et al.*, 1980; Hairston, 1981) the two questions are not directly linked, even if there are good theoretical arguments to do so (Roughgarden, 1979). Thus, if co-occurring species are competing (and common biological sense indicates that co-occurring species are likely to affect each other, but see Wise, 1981), it does not require or imply that the patterns at the community level are the results of this competition. If communities are assemblies of co-evolved species (Diamond, 1975; Roughgarden, 1974, 1979; Futuyma, 1979; Ryder *et al*, 1981), the patterns at the community levels are the result of this competition; but alternatively, if communities are more or less fortuitous assemblies of those species that coexist because they are not competitively excluding each other, then the relationship between the two levels is likely to be weak. Evolutionary biologists cannot agree if natural selection gradually produces adaptation, creating species adapted to very specific conditions and resulting in communities of co-evolved interacting species (Diamond, 1975), or if it operates more abruptly, mostly through species selection (eg. competitive exclusion) (Futuyma, 1979).

This latter view may explain the apparent discrepency between the two levels of observations. When examined at the species level, competition is often present and important (Reynoldson and Bellamy, 1971; Heller, 1971; Brown and Davidson, 1977; Inouye, 1978; Brown *et al.*, 1979; Davidson *et al.*, 1980; Hairston, 1980, 1981; Hixon, 1980; Larson, 1980a, 1980b), but when examined at the community level it does not appear to have significant effect (Caswell, 1976; Pielou, 1977, 1978; Connor and Simberloff, 1979; Strong *et al.*, 1979; Simberloff and Connor, 1981; Simberloff and Boecklen, 1981; present study).

In conclusion, the communities of fish do not appear to be in a C-equilibrium state (*sensu* Connell, 1978), as the examination performed at both levels (species and communities) indicated that interspecific competition was not required to explain the

structure of the fish communities on the artificial reefs. Random colonization from the surrounding habitats is the postulated mechanism responsible for the structure of the fish communities on the artificial reefs. Random colonization as a determinant of community structure applies only to the artificial reefs, and is a result of their isolation. It only operates because strong interactions between species are non-existent. The results on these experimental habitats have to be applied to the more natural systems (eg. the rock rubble slope). I believe that absence of interactions on the reefs generally represents the conditions in the natural environment.

Conclusions

The communities inhabiting the rock rubble slope can be studied using small artificial structures made of concrete blocks, as the species composition and the density in the two communities were similar.

Clearly, a great deal of habitat selection was taking place among the fish of the reefs. The two variables that I examined (shelter type and vertical elevation) both had an important role to play in this selection, and some of the differences in the relative abundance of the species between the natural habitat and the reefs is the result of this selection. It would be relatively simple, by judicious manipulation of the habitat structure, to determine which factors are controlling habitat selection. An answer to this question would not only be of direct interest in community ecology, but it is of considerable importance in the design of larger structures for recreational fisheries. Based on the present findings, reefs designed to attract rockfishes – the only species of commercial interest in this system – should provide a steep elevation and numerous large holes, preferably narrow, as the rockfish were positively selecting these features on the artificial reefs.

Factors other than microhabitat selection may have been responsible for some of the differences observed between the natural and artificial habitats. Seasonal cycles were dampened from the shallower rock rubble slope to the deeper, more isolated insular reefs, a possible consequence of different cover-seeking behaviour between the two areas. Very little is known about the activity cycles of the fish that colonized the reefs and how environmental factors (eg. temperature, turbidity, turbulence, etc.) affect behaviour. Some work is required in this field before these

questions may be answered.

Compared to systems in tropical or subtropical waters (Talbot *et al.*, 1978; Molles, 1978), the community in Barkley Sound was more constant (both in terms of species present and in the amplitude of the fluctuations). The causes of these differences may not be known until the structuring forces at work in these system are fully understood. A great deal of controversy exists in the literature (Helfman, 1978; Smith; 1978b; Anderson *et al.*, 1980; Sale, 1980b) on what these factors might be in coral reef fish communities, different authors often reaching diametrically opposed conclusions. Authors having performed experimental studies seem to concur, however, that competitive interactions between species are not an important structuring force (Sale, 1975, 1977a, 1977b; Sale and Dybdahl, 1975, 1978; Talbot *et al.*, 1978; Bohnsack and Talbot, 1980)

If this were to be generally the case, coral reef communities and the Barkley Sound reef fish community appear to be organized in relatively similar fashion. I was unable to detect any noticeable effects of interactions between species on the structure of the Barkley Sound fish community (taken here in its narrowest sense, i.e. the presence and abundance of species). I therefore rejected the hypothesis – and the common belief held in ecology (Pianka, 1978) – that the structure of this assemblage of fish was primarily the result of interspecific competition between them. This last result is quite robust, as all other potential factors that may have had an effect (eg. habitat, dispersal, etc) were controlled.

Nonetheless, the demonstration that interactions between species do not have any effect on the distributional patterns, at the scale of the Ross Islets, does not demonstrate that they do not exist. By taking advantages of the natural fluctuations in abundance, the presence of interactions between species became evident, some of which may be attributed to competition, while the nature of most others remains conjectural. Removal experiments are required to elucidate the biological basis of these interactions. The removals of *Sebastes caurinus* and *S. maliger* represent a first step in this direction and this line should be actively pursued in future work, now that the interacting pairs have been identified (Chapter V). Artificial structures, like those used here, would again provide ideal systems to approach these problems, because of

the ease with which the spatial distribution and the habitat use can be accurately estimated and quantified on them. The inconclusiveness of the experiment in the present study was due to the small population size, and in the future, much larger systems should be used.

The lack of effects of these interactions on the community structure, as defined earlier, may indicate that the populations are usually too small in nature for these interactions to have significant effects on population regulation. The number of recruits of many species (eg. *Sebastes auriculatus, S. melanops, S. pinniger, J. zonope*) changed dramatically from year to year (Chapter IV), similarly to what happens on coral reefs (Russell *et al.*, 1977). These have been interpreted by fisheries scientists as indicating strong density independent regulation of populations (Cushing, 1975). Some work on the larval ecology of Pacific Northeast fishes (Marliave, 1975; Richardson and Laroche, 1979; Laroche and Richardson, 1980), has recently been done, but these studies have been of too short duration to determine the mechanisms of population regulation.

If the interpretation of density independent regulation is correct, the populations of the species in question may be limited most of the time by the recruitment process. Experimental manipulations could be easily done to determine if the densities are usually too low in natural populations for interaction to have strong distributional effects.

In conclusion, the artificial reefs used here provided an appropriate tool for the study of a reef fish assemblage. The main community parameters (composition, density, abundance recruitment, and spatial distrubution) were examined and accurately quantified using this system. Further, there was no evidence that interactions between these species, as it is commonly postulated in ecology (Pianka, 1978), had any effects on the patterns of distribution and abundance for the members of this assemblage. In light of the strong yearly fluctuations in recruitment, it appears that fluctuations in recruitment consistently keep the adult populations of these fish at densities too low for interactions to take place, a process similar to Connell's (1978) intermediate disturbance hypothesis. Habitat selection appears to be a more important factor in determining the presence and abundance of species. The type of approach used in

this study should prove valuable in the future to test more specific hypotheses on the role of habitat selection, population density, and interactions between species on the community patterns.

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A. Appendix I: Invertebrates recorded on the reefs

Indentifications were made using the keys in Osburn (1950,1952), Kozloff (1974), Smith and Carlton (1975), Fauchald (1977), and Butler (1980).

PORIFERA

Scypha sp.	6	*Leucosolenia sp.*	6

CNIDARIA

Hydrozoa

Tubularia sp.		*Obelia sp.*	1

Anthozoa

Metridium senile			

NEMERTEA

Micrura wilsoni	8		

MOLLUSCA

Amphineura

Cryptochiton stelleri		*Tonicella lineata*	

Prosobranchia

Haliotis kamtschatkana		*Diodora aspera*	
Astrea gibberosa		*Tegula pulligo*	7
Margarites pupillus		*Calliostoma caniculatum*	6
Polinices lewisii	8,9	*Calliostoma ligatum*	9
Nassarius mendicus		*Amphissa columbiana*	12
Ceratostoma foliatum	1,12	*Acmaea mitra*	7,10

Opisthobranchia

Dirona albolineata		*Dendronotus iris*	
Aeolidea papillosa		or *Antiopella fusca*	
Hermissenda crassicornis		*Aegires albopunctatus*	8
Cadlina luteomarginata		*Archidoris montereyensis*	
Diadula sandiegensis		*Archidoris odhneri*	
Acanthodoris nanaimoensis			

Bivalvia

Pododesmus cepio	6,	*Chlamys hastata*	9,12

ANNELIDA

Phyllodocidae

Phyllodoce (mucosa?)			

Serpulidae

Crucigera irregularis	2	*Serpula vermicularis*	2

Sabellidae

Myxicola infudibulum	8		

ARTHROPODA

Cirripedia

Balanus cariosus	11		

Decapoda: Caridea

Pandalus danae	12	*Eualus pusiolus*	8,9
Pandalus platyceros	12	*Eualus herdmani*	12
Heptacarpus brevirostris	8,9	*Heptacarpus tenuissimus*	8,9

Decapoda: Anomura

Pagurus caurinus	1	*Rhinolithodes wosnessenskii*	17
Pagurus hemphilii	9,12	*Paguristes ulreyi*	7
Pagurus setosus	10,5		

Decapoda: Brachyura

Pugettia producta		*Oregonia gracilis*	
Pugettia gracilis		*Cancer branneri*	
Scyra acutifrons	9	*Cancer productus*	

BRYOZOA

Cyclostomata

Crisia sp.	6	*Heteropora sp.*	5
Tubulipora sp.	1	*Diaperoecia sp.*	6

Cheilostomata

Lyrula hippocrepis	12	*Phidolophora pacifica*	6
Bugula sp.	11		

ECHINODERMATA

Asteroidea

Pteraster tesselatus		*Mediaster aequalis*	
Henricia leviuscula		*Crossaster papposus*	
Pisaster brevispinnis		*Pycnopodia helianthoides*	
Orthasterias koehleri		*Solaster stimpsoni*	

Echinoidea

Strongylocentrotus droebachiensis		*Strongylocentrotus franciscanus*	

Holothuroidea

Parastichopus californicus		*Eupentacta pseudoquinquesemita*	8

CHORDATA

Ascidiacea

Corella willmeriana	7	*Cnemidocarpa finmarkiensis*	1
Boltenia villosa	5	*Pyura haustor*	
Aplidium californicum		*Styela montereyensis*	
Didemnum albidum	8		

B. Appendix II: Detailed sampling results for the transects

Absence is indicated by a dash (–).

Upper rock transect survey results:

Survey number:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Date Day	14	26	12	1	2		10	25	19	9	21	6	3	15	30	15	28	12
Date Month	7	7	8	10	11		12	1	2	3	3	4	5	5	5	6	6	7
Date Year	78	78	78	78	78		78	79	79	79	79	79	79	79	79	79	79	79
Aulorhynchus flavidus	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-
Brachyistius frenatus	-	-	-	-	-		2	-	-	-	-	-	-	1	2	-	-	-
Cymatogaster aggregata	-	-	-	-	-		-	-	-	-	-	-	-	2	10	-	-	-
Rhacochilus vacca	-	-	-	-	-		-	-	-	-	-	-	-	-	2	-	-	-
Anoplarchus spp.	-	-	-	-	-		1	-	-	-	-	-	-	-	-	-	-	-
Apodichthys flavidus	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-
Chirolophis spp.	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	1	-
Anarrhichthys ocellatus	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-
Coryphopterus nicholsi	309	299	232	155	136		57	13	9	6	14	14	126	168	149	91	202	209
Sebastes auriculatus	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-
Sebastes caurinus	-	1	1	8	2		-	1	1	-	-	-	7	9	4	2	2	2
Sebastes maliger	13	4	4	8	7		1	1	-	-	-	-	5	12	8	5	8	9
Sebastes melanops	4	4	2	20	8		3	1	-	-	-	1	9	8	12	7	7	2
Sebastes pinniger	-	1	-	2	1		-	-	-	-	-	-	-	-	-	-	-	-
Sebastes spp.	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-
Hexagrammos decagrammus	13	8	5	2	2		4	-	1	-	2	1	3	5	10	4	7	16
Hexagrammos stelleri	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-
Ophiodon elongatus	1	7	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-
Oxylebius pictus	2	3	3	5	1		-	-	-	-	-	-	1	-	-	-	-	-
Artedius spp.	-	1	-	-	-		-	-	-	1	-	-	-	-	-	-	-	-
Hemilepidotus hemilepidotus	1	-	-	-	-		-	-	-	1	-	-	-	-	-	-	-	-
Jordania zonope	-	-	4	1	-		-	-	-	-	-	-	1	2	-	-	3	1
Synchirus gilli	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-
Jordania zonope	-	-	1	-	-		-	-	-	-	-	-	-	-	-	-	-	-
Cottidae spp.	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-
Total number of species	7	10	9	9	8		6	4	3	2	2	4	7	7	8	6	8	7
Total number of fish	343	328	254	201	158		68	16	11	7	16	17	152	206	199	110	234	244

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Upper rock transect survey results, continued.

Survey number:		19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	Total
Date	Day	26	23	23	4	5	25	11	22	5	20	2	16	30	15	28	10	
	Month	7	8	1	2	3	3	4	4	5	5	6	6	6	7	7	8	
	Year	79	79	80	80	80	80	80	80	80	80	80	80	80	80	80	80	
Aulorhynchus flavidus		-	-	-	-	-	-	-	-	-	-	25	-	4	54	55	10	98
Brachyistius frenatus		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5
Cymatogaster aggregata		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12
Rhacochilus vacca		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Anoplarchus spp.		-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	2
Apodichthys flavidus		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Chirolophis pp.		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Pholis laeta		-	1	-	-	-	-	-	-	-	1	2	-	-	-	-	-	8
Anarrhichthys ocellatus		-	3	-	-	-	-	1	-	-	-	-	-	1	1	-	1	7
Coryphopterus nicholsi		181	292	119	87	199	43	88	85	113	68	35	73	101	82	62	53	3870
Sebastes auriculatus		-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1
Sebastes caurinus		4	11	4	2	3	1	2	2	-	1	-	1	2	-	-	-	73
Sebastes maliger		8	14	1	1	1	1	1	2	2	1	1	1	8	1	-	-	128
Sebastes melanops		55	4	10	3	5	1	-	4	1	3	1	1	1	15	30	22	244
Sebastes pinniger		-	-	-	-	-	-	-	-	-	-	-	-	3	5	28	19	69
Sebastes spp.		-	-	-	-	-	1	-	-	1	-	-	-	-	2	-	6	10
Hexagrammos decagrammus		10	6	4	3	5	2	2	2	1	8	2	6	3	2	11	8	161
Hexagrammos stelleri		-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1
Ophiodon elongatus		1	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	11
Oxylebius pictus		6	3	-	2	2	1	2	3	2	1	-	-	2	3	1	1	60
Artedius spp.		-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	15
Hemilepidotus hemilepidotus		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Jordania zonope.		2	-	-	-	-	2	-	-	-	1	-	-	2	1	-	1	21
Synchirus gilli		-	-	-	-	-	-	-	-	-	-	-	3	6	1	-	-	10
Cottidae spp.		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Total number of fish		216	334	138	99	215	52	96	100	122	86	68	86	128	172	139	121	4813
Total number of species		8	8	5	7	6	6	6	8	8	10	8	6	10	11	8	8	23

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Lower transect survey results:

Survey number:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Date Day	6	24	9	29	1	16	10	25	19	3	21	6	3	15	30	15	29	12
Date Month	7	7	8	9	11	11	12	1	2	3	3	4	5	5	5	6	6	7
Date Year	78	78	78	78	78	78	78	79	79	79	79	79	79	79	79	79	79	79
Aulorhynchus flavidus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chirolophis spp.	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pholis laeta	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-
Anarrhichthys ocellatus	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Coryphopterus nicholsi	188	221	133	116	178	63	48	37	23	16	44	44	141	207	200	184	220	274
Sebastes caurinus	-	-	1	-	2	4	-	-	1	-	1	-	-	-	1	-	1	1
Sebastes maliger	-	2	1	2	-	2	2	-	-	-	-	1	3	4	2	2	2	5
Sebastes melanops	1	-	-	2	1	-	-	-	-	-	-	-	2	-	-	-	-	1
Sebastes pinniger	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Hexagrammos decagrammus	11	12	7	3	1	5	1	2	-	1	1	-	-	3	6	-	2	5
Ophiodon elongatus	1	1	4	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-
Oxylebius pictus	-	-	1	1	-	-	-	-	-	-	-	1	-	1	1	-	1	-
Artedius spp.	1	-	-	1	-	-	-	-	-	-	3	-	-	4	1	1	-	-
Enophrys bison	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hemilepidotus hemilepidotus	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Jordania zonope	2	-	1	1	5	-	-	-	-	-	-	-	1	1	1	-	-	-
Rhamphocottus richardsoni	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Synchirus gilli	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cottidae spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Total number of fish	203	242	148	128	186	75	51	40	24	17	51	46	147	220	212	186	226	287
Total number of species	6	6	7	8	6	5	3	3	2	2	6	3	4	7	7	5	5	6

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Lower transect survey results, continued:

Survey number:		19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	Total
Date	Day	26	23	23	4	5	25	11	23	5	20	2	16	30	15	28	10	
	Month	7	8	1	2	3	3	4	4	5	5	6	6	6	7	7	8	
	Year	79	79	80	80	80	80	80	80	80	80	80	80	80	80	80	80	
Aulorhynchus flavidus		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
Chirolophis spp.		-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	2
Pholis laeta		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	4
Anarrhychthys ocellatus		-	3	-	-	-	-	-	-	-	-	-	-	-	-	1	1	10
Coryphopterus nicholsi		284	338	152	105	185	146	108	136	191	219	291	374	426	333	219	264	6088
Sebastes caurinus		2	3	-	-	1	2	-	-	-	-	-	-	1	1	1	1	25
Sebastes maliger		2	9	1	1	2	4	1	4	3	-	3	1	5	2	-	-	66
Sebastes melanops		2	13	-	1	2	-	-	1	2	-	-	-	2	-	4	9	45
Sebastes pinniger		-	1	1	1	-	-	-	-	-	-	-	-	-	-	162	88	256
Hexagrammos decagrammus		4	5	1	-	3	-	-	-	-	3	1	1	3	8	2	1	92
Ophiodon elongatus		-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9
Oxylebius pictus		-	-	1	-	-	-	-	-	1	1	4	1	1	2	3	3	23
Artedius spp.		-	-	-	-	-	-	-	-	-	-	-	-	1	3	1	-	16
Enophrys bison		-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1
Hemilepidotus hemilepidotus		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Jordania zonope		4	-	-	-	-	-	-	-	2	-	5	7	8	1	5	-	40
Rhamphocottus richardsoni		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Synchirus gilli		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	11
Cottidae spp.		-	-	-	-	-	1	-	-	1	1	-	-	-	1	1	4	11
Total number of fish		298	381	152	109	193	153	109	142	200	225	304	384	448	351	400	373	6693
Total number of species		6	8	5	5	5	4	2	4	6	5	5	5	9	7	10	9	18

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Sand transect survey results:

Survey number:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Date Day	15		9			16		25		9	21	6	4	15	30		28	
Date Month	7		8			11		1		3	3	4	5	5	5		6	
Date Year	78		78			78		79		79	79	79	79	79	79		79	
Hydrolagus colliei	3		-			-		-		-	-	-	2	-	1		-	
Coryphopterus nicholsi	-		-			-		-		-	-	-	-	-	-		-	
Sebastes caurinus	2		-			-		-		-	-	-	-	-	-		-	
Sebastes melanops	2		5			-		-		-	-	-	1	-	-		-	
Sebastes pinniger	9		1			-		-		-	-	-	-	-	-		-	
Sebastes spp.	-		-			-		-		-	-	-	-	-	-		-	
Hexagrammos decagrammus	13		9			1		3		-	2	-	-	1	-		4	
Ophiodon elongatus	-		-			-		-		-	1	-	1	-	-		-	
Cottidae spp.	-		-			-		-		-	-	-	-	-	-		-	
Lepidopdetta bilineata	1		1			-		-		-	-	-	-	-	-		1	
Total number of fish	30		16			1		3		0	3	0	4	1	2		7	
Total number of species	6		4			1		1		0	2	0	3	1	2		3	

Sand transect survey results, continued:

Survey number:		19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	Total
Date	Day	26	23	23	4	5	25	15	23	7	16	30	15	30	15	25	10	
	Month	7	8	1	2	3	3	4	4	5	5	5	6	6	7	7	8	
	Year	79	79	80	80	80	80	80	80	80	80	80	80	80	80	80	80	
Hydrolagus colliei		-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	7
Coryphopterus nicholsi		-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	2
Sebastes caurinus		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Sebastes melanops		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9
Sebastes pinniger		2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12
Sebastes spp.		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
Hexagrammos decagrammus		7	4	-	2	1	2	-	-	1	4	7	2	2	3	2	3	73
Ophiodon elongatus		-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	4
Cottidae spp.		-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	2
Lepidopsetta bilineata		1	3	1	-	1	-	-	1	-	1	-	-	-	-	-	-	13
Total number of fish		11	8	1	2	2	2	0	1	2	6	9	3	2	3	2	4	134
Total number of species		4	3	1	1	2	1	0	1	2	3	3	2	1	1	1	2	9

C. Appendix III: Detailed colonization histories of individual reefs

The indented entries represent subtotals within the listings; They are not included in the final totals. To facilitate the reading of the table, dashes (–) are used in the listings before the first sighting of a species on a reef. After a species has been recorded once, absence is indicated by a zero.

Colonization history of reef number 1

Survey number:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Weeks of colonization:	2	5	7	9	11	13	15	17	19	21	23	25	27	29	32	35	38	40
*Porichthys notatus**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gobiesox maeandricus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
*Meluccius productus**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
*Brachyistius frenatus**	-	-	-	-	-	-	-	-	-	-	-	-	1	3	0	0	0	0
*Rhacochilus vacca**	-	-	-	-	-	-	-	-	-	-	2	1	2	1	0	0	0	0
Pholis ornata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Anarrhichthys ocellatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Coryphopterus nicholsi	1	3	3	3	5	3	5	7	1	3	8	8	7	7	9	16	10	11
Sebastes caurinus	-	1	1	1	1	2	3	2	4	1	0	1	1	0	1	2	0	2
Sebastes maliger	1	1	1	0	2	1	4	2	5	2	1	0	2	0	0	1	0	4
Non-schooling *S. melanops*	-	-	-	-	-	-	-	4	0	2	4	8	7	14	7	12	5	2
Schooling *S.melanops**	-	-	-	-	-	-	-	6	60	100	100	40	50	8	0	0	0	0
Sebastes melanops	-	-	-	-	-	-	-	10	60	102	104	48	57	22	7	12	5	2
Sebastes mystinus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sebastes pinniger	-	-	-	-	-	-	-	-	-	-	-	5	2	0	0	0	6	5
Sebastes spp.	-	-	-	-	-	1	0	0	0	1	1	1	0	0	0	0	0	0
Sebastes : Total	1	2	2	1	3	3	7	14	69	105	105	54	62	22	8	15	11	13
Hexagrammos decagrammus	-	-	-	-	-	2	1	2	2	2	4	3	3	2	4	2	2	1
Ophiodon elongatus	-	-	-	-	-	-	-	-	-	-	-	1	0	0	0	0	0	0
Oxylebius pictus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Artedius spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Artedius lateralis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Clinocottus spp.	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Jordania zonope	-	-	-	-	-	-	-	1	0	0	0	0	0	0	0	0	0	0
Cottidae spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cottidae: Total	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0
*Lepidopsetta bilineata**	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pleuronectidae spp.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Number of resident species	3	3	3	3	4	4	4	6	4	5	4	6	6	3	4	5	4	6
Number of resident fish	3	5	5	5	9	9	13	18	12	11	18	27	22	23	21	33	23	25
Total number of fish	4	5	5	5	9	9	13	24	72	111	120	68	75	35	21	33	23	25

*: Non-resident species

Colonization history of reef number 1 continued.

Survey number:	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Weeks of colonization:	42	47	51	53	55	57	59	64	63	65	67	69	71	73	75	77	79	83
*Porichthys notatus**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	0	0
Gobiesox maeandricus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	0	0
*Meluccius productus**	-	-	-	-	-	-	-	-	-	-	1	0	0	0	0	0	0	0
*Brachyistius frenatus**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
*Rhacochilus vacca**	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Pholis ornata	-	-	-	-	-	-	-	-	1	0	0	0	0	0	0	0	0	0
Anarrhichthys ocellatus	-	-	-	-	-	-	-	1	0	0	0	0	0	0	0	0	0	0
Coryphopterus nicholsi	6	8	5	5	9	7	2	7	5	5	6	4	5	14	8	13	9	10
Sebastes caurinus	0	1	1	0	1	1	0	3	2	1	1	3	4	4	3	2	2	2
Sebastes maliger	1	0	0	0	0	0	0	0	0	1	3	5	0	2	2	0	1	1
Non-schooling *S. melanops*	2	0	0	0	1	1	0	0	0	0	0	2	2	3	8	5	6	2
Schooling *S.melanops**	0	0	0	0	0	0	0	0	0	0	0	20	0	50	50	39	0	15
Sebastes melanops	2	0	0	0	1	1	0	0	0	0	0	22	2	53	58	44	6	17
Sebastes mystinus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Sebastes pinniger	3	4	0	1	0	0	0	1	0	0	0	0	0	0	1	0	3	0
Sebastes spp.	1	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	1
Sebastes : Total	6	5	1	1	2	2	0	4	2	2	4	30	6	59	64	46	12	21
Hexagrammos decagrammus	2	1	0	0	0	1	1	2	1	1	2	1	1	3	3	3	2	2
Ophiodon elongatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxylebius pictus	-	-	-	-	-	-	1	0	0	0	0	0	0	1	0	0	0	1
Artedius spp.	-	-	-	-	-	-	1	1	0	0	0	0	0	0	0	0	0	0
Artedius lateralis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Clinocottus spp.	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Jordania zonope	0	0	0	1	0	1	0	2	1	1	1	1	0	1	0	1	0	1
Cottidae spp.	-	-	-	-	-	-	-	-	1	0	0	0	0	0	0	0	0	0
Cottidae: Total	0	0	0	1	0	2	1	3	2	1	1	1	0	1	0	1	0	1
*Lepidopsetta bilineata**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pleuronectidae spp.*	-	-	-	-	-	1	0	1	0	0	0	0	0	0	0	1	0	0
Number of resident species	5	4	2	3	3	6	4	7	5	5	5	6	4	7	7	5	6	8
Number of resident fish	15	14	6	7	12	12	6	18	12	9	13	16	12	28	26	24	23	21
Total number of fish	15	14	7	7	12	13	6	19	12	9	14	36	12	78	77	64	23	37

*: Non-resident species

Colonization history of reef number 1 continued.

Survey number:	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	to-
Weeks of colonization:	88	94	99	101	103	106	108	110	112	114	116	118	120	122	124	126	128	130	tal
*Porichthys notatus**	0	0	0	0	0														1
Gobiesox maeandricus	0	0	0	0	0														1
*Meluccius productus**	0	0	0	0	0														1
*Brachyistius frenatus**	0	0	0	0	0														4
*Rhacochilus vacca**	0	0	0	0	0														8
Pholis ornata	0	0	0	0	0														1
Anarrhichthys ocellatus	0	0	0	0	0														1
Coryphopterus nicholsi	16	12	29	25	20														340
Sebastes caurinus	0	0	1	2	1														58
Sebastes maliger	2	3	3	2	1														54
Non-schooling *S. melanops*	3	8	5	6	1														120
Schooling *S.melanops**	10	0	0	0	0														548
Sebastes melanops	13	8	5	6	1														668
Sebastes mystinus	0	0	0	0	0														1
Sebastes pinniger	2	5	5	5	0														48
Sebastes spp.	0	0	0	0	0														10
Sebastes : Total	17	16	14	15	3														829
Hexagrammos decagrammus	2	2	2	1	0														63
Ophiodon elongatus	0	0	0	0	0														1
Oxylebius pictus	0	0	1	1	0														5
Artedius spp.	0	0	0	0	0														2
Artedius lateralis	-	-	1	0	0														1
Clinocottus spp.	0	0	0	0	0														4
Jordania zonope	0	0	0	0	0														12
Cottidae spp.	0	0	0	0	0														1
Cottidae: Total	0	0	1	0	0														20
*Lepidopsetta bilineata**	0	0	0	0	0														1
Pleuronectidae spp.*	0	0	0	0	0														3
Number of resident species	5	5	8	7	4														16
Number of resident fish	25	30	47	42	23														723
Total number of fish	35	30	47	42	23														1289

*: Non-resident species

Colonization history of reef number 2

Survey number:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Weeks of colonization:	2	5	7	9	11	13	15	17	19	21	23	25	27	29	32	35	38	40
*Rhacochilus vacca**	-	-	-	-	-	-	-	-	-	-	-	-	3	0	0	0	0	0
Pholis sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Anoplarchus purpurescens	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Anarrhichthys ocellatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Coryphopterus nicholsi	-	-	1	2	1	3	1	0	1	3	1	0	4	0	2	4	5	6
Sebastes auriculatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sebastes caurinus	-	1	1	2	2	4	3	2	2	1	2	5	8	1	4	1	0	2
Sebastes maliger	-	-	1	1	0	0	1	7	7	5	1	0	2	4	1	2	8	3
Non-schooling *S. melanops*	-	-	-	-	-	-	-	-	-	-	1	7	5	6	9	7	8	2
Schooling *S.melanops**	-	-	-	-	-	-	-	-	-	-	8	0	30	12	0	12	0	0
Sebastes melanops	-	-	-	-	-	-	-	-	-	-	9	7	35	18	9	19	8	2
Sebastes pinniger	-	-	-	-	-	-	-	-	-	-	-	3	0	5	6	6	4	3
Sebastes spp.	2	1	0	0	0	0	1	0	0	1	0	0	2	0	1	2	0	0
Sebastes : Total	-	1	2	3	2	4	4	9	9	6	12	15	45	28	20	28	20	10
Hexagrammos decagrammus	-	-	-	-	-	-	1	1	0	0	0	1	2	1	1	3	2	2
Oxylebius pictus	-	-	-	-	-	-	-	-	1	0	0	0	0	0	0	0	0	0
Artedius spp.	-	-	-	-	-	-	-	-	-	-	-	1	1	1	0	0	0	2
Clinocottus spp.	3	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	1	0
Jordania zonope	-	-	-	-	-	-	-	-	-	-	-	1	0	0	0	0	0	0
Rhamphocottus richardsoni	-	-	-	-	-	-	-	-	-	-	-	-	1	0	0	0	0	0
Cottidae spp.	-	-	-	2	0	0	0	0	1	1	0	1	0	0	0	1	0	1
Cottidae: Total	3	0	0	3	1	1	1	1	2	1	0	3	2	1	0	1	1	3
*Lepidopsetta bilineata**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Number of resident species	1	2	3	4	3	3	5	4	5	4	4	6	7	6	6	7	6	7
Number of resident fish	5	2	3	8	4	8	8	11	13	11	5	19	25	18	24	26	28	21
Total number of fish	5	2	3	8	4	8	8	11	13	11	13	19	58	30	24	38	28	21

*: Non-resident species

Colonization history of reef number 2 continued.

Survey number:	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Weeks of colonization:	42	47	51	53	55	57	59	61	63	65	67	69	71	73	75	77	79	83
*Rhacochilus vacca**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholis sp.	-	-	-	1	0	0	0	0	2	0	0	0	0	0	0	1	0	0
Anoplarchus purpurescens	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Anarrhichthys ocellatus	-	-	-	-	-	-	-	1	0	0	0	0	0	2	1	0	0	0
Coryphopterus nicholsi	6	7	4	7	8	9	12	10	9	5	4	3	4	10	14	11	16	11
Sebastes auriculatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sebastes caurinus	1	1	0	0	3	1	3	5	4	1	1	2	1	1	2	2	0	1
Sebastes maliger	5	4	2	5	4	5	1	5	1	4	4	7	5	3	2	3	2	7
Non-schooling *S. melanops*	9	0	1	1	5	2	1	5	3	2	6	4	3	4	4	7	0	4
Schooling *S.melanops**	0	0	0	0	0	0	0	0	0	0	0	0	40	27	20	100	22	0
Sebastes melanops	9	0	1	1	5	2	1	5	3	2	6	4	43	31	24	107	22	4
Sebastes pinniger	3	2	1	0	3	0	0	0	0	0	0	0	0	0	1	0	0	0
Sebastes spp.	0	0	0	0	0	1	1	0	1	2	0	1	1	0	1	0	0	3
Sebastes : Total	18	7	4	6	15	8	5	15	8	7	11	13	49	35	29	112	24	12
Hexagrammos decagrammus	2	1	1	0	2	1	1	2	2	0	1	1	1	2	2	1	0	0
Oxylebius pictus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artedius spp.	1	1	0	1	0	1	1	0	1	2	3	3	2	3	1	4	3	2
Clinocottus spp.	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Jordania zonope	0	0	0	0	0	0	1	3	1	2	2	4	2	0	2	4	1	1
Rhamphocottus richardsoni	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cottidae spp.	0	0	0	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0
Cottidae: Total	1	1	0	2	1	3	2	4	2	4	6	8	4	3	3	8	4	3
*Lepidopsetta bilineata**	-	-	-	-	-	-	1	0	0	0	0	0	0	0	0	0	0	0
Number of resident species	7	6	5	5	7	7	7	8	8	6	7	7	7	7	9	8	4	6
Number of resident fish	27	16	9	16	26	22	21	32	24	18	22	26	19	25	30	33	22	29
Total number of fish	27	16	9	16	26	22	22	32	24	18	22	26	59	52	50	133	44	29

*: Non-resident species

Colonization history of reef number 2 continued.

Survey number:	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	to-
Weeks of colonization:	88	94	99	101	103	106	108	110	112	114	116	118	120	122	124	126	128	130	tal
*Rhacochilus vacca**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Pholis sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	5
Anoplarchus purpurescens	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	0	0	0	1
Anarrhichthys ocellatus	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	2	9
Coryphopterus nicholsi	17	11	24	22	6	16	20	21	18	17	22	17	13	14	11	8	9	7	457
Sebastes auriculatus	-	-	-	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	3
Sebastes caurinus	2	0	0	1	0	0	0	0	0	0	0	0	2	2	2	2	2	2	85
Sebastes maliger	10	9	8	9	1	4	4	3	1	1	3	1	6	7	1	6	5	5	196
Non-schooling *S. melanops*	6	12	10	7	4	2	3	1	1	2	0	1	1	2	0	3	1	0	162
Schooling *S.melanops**	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	281
Sebastes melanops	6	12	10	17	4	2	3	1	1	2	0	1	1	2	0	3	1	0	443
Sebastes pinniger	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	38
Sebastes spp.	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	23
Sebastes : Total	18	21	18	29	5	6	7	4	2	3	3	2	10	11	3	12	8	7	765
Hexagrammos decagrammus	0	0	1	1	1	1	1	1	0	1	1	2	0	0	0	1	0	0	45
Oxylebius pictus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Artedius spp.	2	0	2	2	0	0	0	0	1	1	1	0	2	1	1	1	1	1	50
Clinocottus spp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	14
Jordania zonope	1	0	1	1	3	1	3	2	2	1	4	3	4	5	5	1	4	5	70
Rhamphocottus richardsoni	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	4
Cottidae spp.	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	15
Cottidae: Total	4	0	3	4	3	2	4	3	3	2	5	4	6	6	7	2	5	7	153
*Lepidopsetta bilineata**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Number of resident species	6	3	6	11	5	6	7	7	5	6	5	5	7	7	6	9	7	6	15
Number of resident fish	39	32	46	47	15	25	33	30	23	24	31	26	29	32	21	24	23	23	1179
Total number of fish	39	32	46	57	15	25	33	30	23	24	31	26	29	32	21	24	23	23	1464

*: Non-resident species

Colonization history of reef number 3

Survey number:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Weeks of colonization:	2	5	7	9	11	13	15	17	19	21	23	25	27	29	32	35	38	40
Gobiesox maeandricus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
*Rhacochilus vacca**	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	0	0	0
Pholis laeta	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	0	0	0
Pholis ornata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pholis sp.	-	-	-	-	-	1	0	0	0	0	0	0	0	0	0	0	0	0
Xiphister mucosus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Anarrhichthys ocellatus	-	-	-	-	-	-	-	-	-	1	0	0	0	1	1	2	0	0
Coryphopterus nicholsi	1	0	0	2	3	2	2	1	4	2	5	2	8	3	5	5	9	7
Sebastes auriculatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sebastes caurinus	-	4	2	1	1	1	2	1	4	4	1	2	2	2	1	1	0	1
Sebastes maliger	1	0	0	1	1	1	4	3	5	1	1	0	3	1	0	2	4	3
Non-schooling *S. melanops*	-	-	-	-	-	1	0	0	2	3	7	6	9	6	11	7	7	2
Schooling *S.melanops**	-	-	-	-	-	-	6	60	0	0	0	30	0	7	0	0	0	0
Sebastes melanops	-	-	-	-	-	1	6	60	2	3	7	36	9	13	11	7	7	2
Sebastes pinniger	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	1	4	2
Sebastes spp.	-	-	-	-	-	1	0	0	0	0	0	2	1	1	0	0	0	0
Sebastes : Total	1	4	2	2	2	3	12	64	11	8	9	38	14	16	17	11	15	8
Hexagrammos decagrammus	-	-	-	-	-	-	-	1	2	2	3	2	4	4	0	0	2	1
Ophiodon elongatus	-	-	-	-	-	-	-	-	-	-	-	-	1	0	0	0	0	0
Artedius spp.	-	-	-	1	0	0	0	0	0	0	1	0	0	1	1	0	0	0
Clinocottus spp.	2	2	3	2	0	1	0	0	2	1	0	0	1	0	0	0	0	0
Hemilepidotus hemilepidotus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	0
Jordania zonope	-	-	-	-	-	-	-	-	-	1	0	0	0	0	0	0	0	0
Rhamphocottus richardsoni	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cottidae spp.	-	-	-	-	-	-	-	1	0	0	0	0	1	0	0	0	0	0
Cottidae: Total	2	2	3	3	0	1	0	1	2	2	1	0	2	1	1	1	0	0
*Lepidopsetta bilineata**	-	-	-	-	-	-	-	-	-	1	0	1	0	0	0	0	0	0
*Pleuronichthys coenosus**	-	-	-	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pleuronectidae spp.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Number of resident species	3	2	2	5	3	6	3	5	6	8	6	4	7	8	6	7	5	6
Number of resident fish	4	6	5	7	5	8	8	7	19	15	18	14	30	20	24	19	26	16
Total number of fish	4	6	5	8	5	8	14	67	19	16	18	45	30	28	24	19	26	16

*: Non-resident species

Colonization history of reef number 3 continued.

Survey number:	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Weeks of colonization:	42	47	51	53	55	57	59	61	63	65	67	69	71	73	75	77	79	83
Gobiesox maeandricus	-	-	-	-	-	-	1	0	0	0	0	0	0	0	0	0	0	0
*Rhacochilus vacca**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholis laeta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholis ornata	-	-	-	-	-	-	-	-	-	-	1	0	0	0	0	0	0	0
Pholis sp.	0	0	0	0	0	0	0	0	0	1	0	0	0	2	2	0	0	0
Xiphister mucosus	-	-	-	-	-	1	0	0	0	0	0	0	0	0	0	0	0	0
Anarrhichthys ocellatus	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	1	1	1
Coryphopterus nicholsi	6	5	7	3	1	5	5	4	7	9	7	5	3	6	11	8	12	14
Sebastes auriculatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sebastes caurinus	2	2	1	1	1	1	0	0	1	1	3	1	2	4	5	1	2	1
Sebastes maliger	4	1	0	0	0	0	0	2	2	7	5	3	3	6	3	0	1	0
Non-schooling *S. melanops*	3	0	1	2	3	0	0	1	1	0	0	0	0	0	2	2	2	0
Schooling *S.melanops**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sebastes melanops	3	0	1	2	3	0	0	1	1	0	0	0	0	0	2	2	2	0
Sebastes pinniger	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sebastes spp.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Sebastes: Total	11	3	3	4	4	1	0	3	4	8	8	4	5	10	10	3	5	1
Hexagrammos decagrammus	0	2	0	1	1	1	1	1	0	1	1	2	1	1	3	2	2	3
Ophiodon elongatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artedius spp.	0	1	0	0	1	0	0	0	0	0	0	1	2	0	2	0	0	0
Clinocottus spp.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Hemilepidotus hemilepidotus	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Jordania zonope	0	1	0	0	0	0	0	0	1	1	1	0	0	0	1	0	1	1
Rhamphocottus richardsoni	-	-	-	-	-	-	-	-	-	-	-	-	1	2	0	0	0	1
Cottidae spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cottidae: Total	0	2	0	0	1	0	0	0	1	2	1	1	4	2	3	0	1	2
*Lepidopsetta bilineata**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
*Pleuronichthys coenosus**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pleuronectidae spp.*	-	-	-	-	-	-	-	1	0	0	0	0	0	0	0	0	0	0
Number of resident species	5	6	4	6	6	5	3	4	5	7	6	5	7	6	9	5	7	6
Number of resident fish	17	12	10	9	8	9	7	8	12	21	18	12	14	21	30	14	21	21
Total number of fish	17	12	10	9	8	9	7	9	12	21	18	12	14	21	30	14	21	21

*: Non-resident species

Colonization history of reef number 3 continued.

Survey number:	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	to-
Weeks of colonization:	88	94	99	101	103	106	108	110	112	114	116	118	120	122	124	126	128	130	tal
Gobiesox maeandricus	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	1
*Rhacochilus vacca**	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	1
Pholis laeta	0	0	1	0	0	0		0	0	0	0	0	0	0	0	0	0	0	2
Pholis ornata	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	1
Pholis sp.	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	6
Xiphister mucosus	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	1
Anarrhichthys ocellatus	0	0	0	0	0	0		0	0	0	1	0	0	0	0	0	0	0	13
Coryphopterus nicholsi	11	7	10	6	10	5		6	5	9	9	1	8	13	7	7	7	10	310
Sebastes auriculatus	-	-	-	-	-	-		-	-	-	-	-	-	-	2	0	0	0	2
Sebastes caurinus	1	0	0	0	0	0		0	0	1	1	7	1	1	3	0	2	1	77
Sebastes maliger	1	2	3	3	0	0		0	1	0	1	1	1	5	3	0	1	2	92
Non-schooling *S. melanops*	2	0	1	1	1	0		0	0	2	0	0	0	0	0	0	0	0	85
Schooling *S.melanops**	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	103
Sebastes melanops	2	0	1	1	1	0		0	0	2	0	0	0	0	0	0	0	0	188
Sebastes pinniger	0	0	0	0	0	0		0	0	0	1	0	0	0	0	0	0	0	17
Sebastes spp.	0	0	0	0	0	0		0	0	0	0	0	0	0	0	1	0	0	7
Sebastes : Total	4	2	4	4	1	0		0	1	3	3	8	2	6	8	0	3	3	376
Hexagrammos decagrammus	2	1	2	1	0	1		0	2	1	2	0	0	0	1	1	1	0	59
Ophiodon elongatus	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	1
Artedius spp.	0	0	0	0	0	0		1	0	1	1	1	1	2	1	1	2	2	24
Clinocottus spp.	0	0	0	0	0	0		0	1	0	0	0	0	0	0	0	0	0	16
Hemilepidotus hemilepidotus	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	2
Jordania zonope	0	0	0	0	0	0		0	0	0	0	0	0	3	2	5	5	5	28
Rhamphocottus richardsoni	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	4
Cottidae spp.	0	0	0	0	0	0		0	0	1	0	0	0	1	1	0	0	0	5
Cottidae: Total	0	0	0	0	0	0		1	1	2	1	1	1	6	4	6	7	7	79
*Lepidopsetta bilineata**	1	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	3
*Pleuronichthys coenosus**	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	1
Pleuronectidae spp.*	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	1
Number of resident species	5	3	5	4	2	2		2	4	5	7	4	4	5	7	4	6	5	19
Number of resident fish	17	10	17	11	11	6		7	9	15	16	10	11	25	20	15	18	20	753
Total number of fish	18	10	17	11	11	6		7	9	15	16	10	11	25	20	15	18	20	862

*: Non-resident species

Colonization history of reef number 4

Survey number:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Weeks of colonization:	2	5	7	9	11	13	15	17	19	21	23	25	27	29	32	35	38	40
Gobiesox maeandricus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
*Rhacochilus vacca**	-	-	-	-	-	-	-	-	-	-	-	-	1	3	0	0	0	0
Pholis ornata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pholis sp.	-	-	-	-	-	-	-	1	1	0	0	0	0	0	0	0	0	0
Blennioidei spp.	-	-	-	-	-	-	1	0	0	0	0	0	0	0	0	0	0	0
Anarrhichthys ocellatus	-	-	-	-	-	-	-	-	-	1	0	0	1	1	0	0	0	0
Coryphopterus nicholsi	1	1	1	1	0	1	1	1	1	2	0	3	2	4	4	6	6	10
Sebastes auriculatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sebastes caurinus	1	1	1	1	0	3	1	4	6	1	0	2	0	1	2	3	1	2
Sebastes maliger	-	1	1	2	0	1	5	3	2	3	0	1	1	2	2	1	2	2
Non-schooling *S. melanops*	-	-	-	-	-	-	-	2	9	9	7	13	15	3	7	5	4	5
Schooling *S.melanops**	-	-	-	-	-	-	-	65	15	36	0	15	25	15	22	14	6	0
Sebastes melanops	-	-	-	-	-	-	-	67	24	45	7	28	40	18	29	19	10	5
Sebastes pinniger	-	-	-	-	-	-	-	-	-	-	-	1	0	0	4	0	2	5
Sebastes spp.	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0
Sebastes : Total	1	2	2	3	0	4	6	74	32	49	7	32	41	21	37	23	15	14
Hexagrammos decagrammus	-	-	-	-	-	-	1	2	2	1	2	2	3	2	1	0	0	1
Ophiodon elongatus	-	-	-	-	-	-	-	-	1	0	0	0	0	0	0	0	0	0
Artedius spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	2
Clinocottus spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Jordania zonope	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nautichthys occulofasciatus	-	-	-	-	-	-	1	0	0	0	0	0	0	0	0	0	0	0
Rhamphocottus richardsoni	-	-	-	-	-	1	0	0	0	0	0	1	0	0	0	0	0	0
Cottidae spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cottidae: Total	-	-	-	-	-	1	1	0	0	0	0	1	0	0	0	1	1	2
*Lepidopsetta bilineata**	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Pleuronectidae spp.*	-	-	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Number of resident species	3	3	3	3	0	4	6	6	7	6	2	7	5	6	6	5	6	7
Number of resident fish	3	3	3	4	0	6	10	13	22	18	9	23	23	14	20	16	16	27
Total number of fish	4	3	5	4	0	6	10	78	37	54	9	39	50	32	42	30	22	28

*: Non-resident species

Colonization history of reef number 4 continued.

Survey number:	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Weeks of colonization:	42	47	51	53	55	57	59	61	63	65	67	69	71	73	75	77	79	83
Gobiesox maeandricus	-	-	-	-	-	-	1	0	0	0	0	0	0	0	0	0	0	0
*Rhacochilus vacca**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholis ornata	-	-	-	-	-	-	-	-	-	-	2	0	0	0	0	0	0	0
Pholis sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Blennioidei spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anarrhichthys ocellatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Coryphopterus nicholsi	5	4	5	10	12	6	2	3	10	6	5	5	3	11	8	7	10	8
Sebastes auriculatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Sebastes caurinus	1	3	1	1	1	1	0	0	1	3	2	4	3	3	2	1	1	1
Sebastes maliger	3	4	0	1	4	0	0	1	1	4	5	5	10	8	9	6	7	8
Non-schooling *S. melanops*	6	1	3	4	4	3	1	0	0	0	0	3	2	6	3	1	2	0
Schooling *S.melanops**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sebastes melanops	6	1	3	4	4	3	1	0	0	0	0	3	2	6	3	1	2	0
Sebastes pinniger	4	4	2	2	3	0	0	0	0	0	0	0	0	0	0	0	0	0
Sebastes spp.	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0
Sebastes : Total	14	12	6	8	12	4	1	1	2	7	7	12	15	17	14	8	10	10
Hexagrammos decagrammus	0	1	1	0	2	1	1	0	2	1	0	0	0	1	1	1	1	1
Ophiodon elongatus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Artedius spp.	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0
Clinocottus spp.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jordania zonope	-	1	0	0	0	0	0	0	0	0	0	0	0	2	2	1	1	0
Nautichthys occulofasciatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Rhamphocottus richardsoni	1	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	2	0
Cottidae spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cottidae: Total	3	2	0	0	0	0	0	0	0	0	1	1	1	3	3	1	5	0
*Lepidopsetta bilineata**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pleuronectidae spp.*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Number of resident species	8	8	5	5	6	4	4	2	4	4	5	5	5	9	7	7	9	6
Number of resident fish	22	19	12	18	26	11	5	4	14	15	16	19	19	35	27	18	26	20
Total number of fish	22	19	12	18	26	11	5	4	14	15	16	19	19	35	27	18	26	20

*: Non-resident species

Colonization history of reef number 4 continued.

Survey number:	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	to-
Weeks of colonization:	88	94	99	101	103	106	108	110	112	114	116	118	120	122	124	126	128	130	tal
Gobiesox maeandricus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
*Rhacochilus vacca**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
Pholis ornata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Pholis sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Blennioidei spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Anarrhichthys ocellatus	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	9
Coryphopterus nicholsi	11	8	11	7	14	8	9	6	4	8	9	10	6	9	7	8	11	11	322
Sebastes auriculatus	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	5
Sebastes caurinus	0	0	1	1	1	2	2	0	1	0	1	2	2	3	3	4	1	1	84
Sebastes maliger	7	6	4	5	3	5	5	3	5	4	3	4	8	4	3	6	3	1	184
Non-schooling *S. melanops*	1	2	1	3	0	1	0	0	0	0	0	0	0	0	0	0	0	1	127
Schooling *S.melanops**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	213
Sebastes melanops	1	2	1	3	0	1	0	0	0	0	0	0	0	0	0	0	0	1	340
Sebastes pinniger	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	27
Sebastes spp.	0	0	2	1	1	1	0	1	0	0	0	0	0	0	1	0	1	1	18
Sebastes : Total	9	8	7	9	4	8	7	3	6	4	5	6	10	7	6	11	4	3	640
Hexagrammos decagrammus	4	2	1	0	1	1	0	1	0	1	1	0	0	0	0	0	0	1	44
Ophiodon elongatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Artedius spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	10
Clinocottus spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Jordania zonope	2	0	1	1	1	0	0	1	0	1	2	2	0	2	1	2	3	2	28
Nautichthys oculofasciatus	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	3
Rhamphocottus richardsoni	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8
Cottidae spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	0	0	0	1
Cottidae: Total.	2	0	1	1	1	0	1	1	0	1	2	2	0	3	2	2	3	2	51
*Lepidopsetta bilineata**	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	3
Pleuronectidae spp.*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
Number of resident species	7	4	7	5	5	5	4	4	3	5	6	4	3	5	5	5	5	6	18
Number of resident fish	27	18	22	18	21	18	17	12	10	15	17	18	16	20	16	21	20	18	880
Total number of fish	27	18	22	18	21	18	17	12	11	15	17	18	16	20	16	21	20	18	1104

*: Non-resident species

Colonization history of reef number 5

Survey number:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Weeks of colonization:	0	0	0	0	0	0	0	0	0	0	0	0	1	3	6	9	12	14
*Brachyistius frenatus**													-		-	-	1	1
Pholis laeta													-		-	-	-	-
Anoplarchus insignis													-		-	-	-	-
Anarrhichthys ocellatus													-		-	-	-	-
Coryphopterus nicholsi													-		-	2	4	2
Sebastes auriculatus													-		-	-	-	-
Sebastes caurinus													1		2	1	0	2
Sebastes maliger													1		0	3	2	3
Non-schooling *S. melanops*													2		10	10	6	6
Schooling *S.melanops**													-		-	25	0	0
Sebastes melanops													2		10	35	6	6
Sebastes pinniger													-		-	-	-	3
Sebastes spp.													-		2	4	0	0
Sebastes : Total													4		12	39	8	14
Hexagrammos decagrammus													-		2	2	2	2
Artedius spp.													-		-	-	-	-
Clinocottus spp.													-		-	-	-	2
Jordania zonope													-		-	-	-	-
Rhamphocottus richardsoni													-		-	-	-	-
Scorpaenichthys marmoratus													-		-	-	-	-
Cottidae spp.													-		-	-	-	-
Cottidae: Total													-		-	-	-	2
*Lepidopsetta bilineata**													-		-	-	-	-
Number of resident species													3		3	5	4	7
Number of resident fish													4		16	22	14	20
Total number of fish													4		16	47	15	21

*: Non-resident species

Colonization history of reef number 5 continued.

Survey number:	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Weeks of colonization:	16	21	25	27	29	31	33	35	37	39	41	43	45	47	49	51	53	57
*Brachyistius frenatus**	0	0	3	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholis laeta	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Anoplarchus insignis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Anarrhichthys ocellatus	-	-	-	-	-	-	-	-	-	-	-	-	1	0	1	1	0	0
Coryphopterus nicholsi	3	1	2	6	9	11	5	9	9	7	7	4	3	5	6	11	10	16
Sebastes auriculatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sebastes caurinus	0	2	2	3	2	1	2	5	4	2	2	6	4	2	2	2	2	0
Sebastes maliger	7	0	0	2	5	2	1	3	2	6	5	6	4	7	4	1	5	4
Non-schooling *S. melanops*	3	2	1	3	2	3	1	1	3	3	1	4	3	9	8	8	9	2
Schooling *S.melanops**	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sebastes melanops	11	2	1	3	2	3	1	1	3	3	1	4	3	9	8	8	9	2
Sebastes pinniger	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Sebastes spp.	1	2	0	0	0	0	0	1	2	2	1	0	2	0	0	1	0	0
Sebastes : Total	19	4	3	9	9	6	4	9	9	11	8	16	11	18	15	11	16	6
Hexagrammos decagrammus	3	4	1	2	2	1	1	2	0	2	1	0	1	1	2	3	0	3
Artedius spp.	-	-	-	-	1	2	0	1	1	3	1	2	0	4	2	5	3	1
Clinocottus spp.	2	1	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0
Jordania zonope	-	-	-	1	1	1	0	0	1	0	1	2	1	1	0	0	1	1
Rhamphocottus richardsoni	-	-	-	-	-	-	-	-	-	-	1	1	0	0	0	0	0	0
Scorpaenichthys marmoratus	-	-	-	-	-	-	1	0	0	0	0	0	0	0	0	0	0	0
Cottidae spp.	-	-	-	-	-	-	-	1	3	0	0	0	1	0	1	0	0	0
Cottidae: Total	2	1	0	2	3	3	1	2	5	4	3	6	2	5	3	5	4	2
*Lepidopsetta bilineata**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Number of resident species	6	5	4	8	8	7	6	6	6	7	8	8	7	7	8	7	6	6
Number of resident fish	20	12	6	19	23	21	11	23	25	26	20	26	20	29	27	32	30	27
Total number of fish	28	12	9	21	25	21	11	23	25	26	20	26	20	29	27	32	30	27

*: Non-resident species

Colonization history of reef number 5 continued.

Survey number:	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	to-
Weeks of colonization:	62	68	73	75	77	80	82	84	86	88	90	92	94	96	98	100	102	104	tal
*Brachyistius frenatus**	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	9
Pholis laeta	-	-	-	-	-		-	1	0	0	0	0	0	0	0	0	0	0	1
Anoplarchus insignis	-	-	-	-	-		-	-	-	1	0	0	0	0	0	0	0	0	1
Anarrhichthys ocellatus	0	0	0	0	0		0	0	0	0	1	1	0	0	0	1	0	0	6
Coryphopterus nicholsi	16	5	19	17	22		9	9	6	8	7	8	7	6	4	7	6	5	293
Sebastes auriculatus	-	1	1	0	1		0	0	0	0	0	0	1	0	0	0	0	0	4
Sebastes caurinus	1	2	2	0	0		1	2	0	1	0	0	4	0	1	2	1	2	68
Sebastes maliger	4	1	3	6	0		4	3	3	3	2	4	4	2	1	4	4	1	122
Non-schooling *S. melanops*	12	6	3	8	5		3	2	3	3	3	1	0	2	2	2	0	1	156
Schooling *S.melanops**	0	10	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	43
Sebastes melanops	12	16	3	8	5		3	2	3	3	3	1	0	2	2	2	0	1	199
Sebastes pinniger	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	6
Sebastes spp.	0	0	1	0	1		0	2	1	0	1	0	0	0	1	0	0	0	25
Sebastes : Total	17	20	9	14	6		8	7	6	7	5	5	9	4	4	8	5	4	399
Hexagrammos decagrammus	1	2	2	1	1		1	0	1	0	0	0	1	0	2	0	0	0	49
Artedius spp.	0	0	1	2	2		2	3	1	1	1	1	2	3	0	2	1	3	51
Clinocottus spp.	0	1	1	1	0		0	0	0	0	0	0	1	0	0	0	0	0	13
Jordania zonope	1	0	0	0	1		0	0	1	0	0	0	2	1	1	3	2	4	27
Rhamphocottus richardsoni	0	0	1	0	0		0	0	0	0	0	0	0	0	0	0	0	1	4
Scorpaenichthys marmoratus	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	1	2
Cottidae spp.	0	0	0	0	1		0	0	0	0	0	0	0	0	1	0	0	0	8
Cottidae: Total	1	1	3	3	4		2	3	2	1	1	1	5	4	2	5	3	9	105
*Lepidopsetta bilineata**	-	-	-	-	-		-	-	1	0	0	0	0	0	0	0	0	0	1
Number of resident species	6	7	9	6	6		6	6	6	6	5	5	8	5	6	7	5	8	15
Number of resident fish	35	18	34	35	34		20	22	16	17	15	15	22	14	13	21	14	18	836
Total number of fish	35	28	34	35	34		20	22	17	17	15	15	22	14	13	21	14	18	889

*: Non-resident species

Colonization history of reef number 6

Survey number:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Weeks of colonization:	0	0	0	0	0	0	0	0	0	0	0	0	1	3	6	9	12	14
Pholis laeta													-	-	-	-		-
Pholis sp.													-	-	-	-		-
Anoplarchus purpurescens													-	-	-	-		-
Blennioidei spp.													-	-	-	-		-
Anarrhichthys ocellatus													-	-	-	-		-
Coryphopterus nicholsi													-	-	5	3		0
Sebastes auriculatus													-	-	-	-		-
Sebastes caurinus													-	-	3	4		3
Sebastes maliger													-	-	-	1		3
Non-schooling *S. melanops*													-	-	1	1		0
Sebastes melanops													-	-	1	1		0
Sebastes pinniger													-	-	-	-		1
Sebastes spp.													-	-	1	0		0
Sebastes : Total													-	-	4	6		7
Hexagrammos decagrammus													1	1	1	1		1
Artedius spp.													-	-	-	-		-
Artedius lateralis													-	-	-	-		1
Clinocottus spp.													1	0	0	0		0
Hemilepidotus hemilepidotus													-	-	-	-		-
Jordania zonope													-	-	-	-		-
Rhamphocottus richardsoni													-	-	-	-		-
Cottidae spp.													-	-	-	-		-
Cottidae: Total													1	0	0	0		1
Pleuronectidae spp.*													-	-	-	-		-
Number of resident species													2	1	4	5		5
Number of resident fish													2	1	11	10		9
Total number of fish													2	1	11	10		9

*: Non-resident species

Colonization history of reef number 6 continued.

Survey number:	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Weeks of colonization:	16	21	25	27	29	31	33	35	37	39	41	43	45	47	49	51	53	57
Pholis laeta	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pholis sp.	-	-	-	-	-	-	-	1	0	0	0	0	0	0	0	0	0	0
Anoplarchus purpurescens	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Blennioidei spp.	-	-	-	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anarrhichthys ocellatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Coryphopterus nicholsi	1	0	2	2	3	3	4	5	6	2	4	3	2	5	5	3	9	5
Sebastes auriculatus	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	0	0	0
Sebastes caurinus	4	3	2	3	4	1	0	3	4	5	6	8	8	4	4	4	1	2
Sebastes maliger	1	2	3	3	5	6	2	4	3	2	3	3	5	10	6	2	2	6
Non-schooling *S. melanops*	1	0	1	1	0	0	1	0	0	0	0	0	0	0	1	2	0	0
Sebastes melanops	1	0	1	1	0	0	1	0	0	0	0	0	0	0	1	2	0	0
Sebastes pinniger	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Sebastes spp.	1	0	1	1	0	0	1	0	1	2	2	0	0	0	0	0	0	0
Sebastes : Total	6	5	6	7	10	8	3	7	7	7	9	11	13	15	12	8	3	8
Hexagrammos decagrammus	3	1	1	3	3	2	2	1	1	0	0	1	0	1	1	1	0	1
Artedius spp.	-	-	-	-	-	-	-	1	0	0	0	0	0	0	0	0	0	0
Artedius lateralis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Clinocottus spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hemilepidotus hemilepidotus	-	-	-	-	-	-	-	-	-	-	-	1	1	0	1	0	0	0
Jordania zonope	-	-	-	-	-	-	-	1	0	0	0	1	1	0	0	0	0	0
Rhamphocottus richardsoni	-	-	-	-	1	0	0	0	0	0	1	0	0	0	0	0	0	0
Cottidae spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0
Cottidae: Total	0	0	0	0	1	0	0	2	0	0	1	2	2	0	1	0	1	0
Pleuronectidae spp.*	-	-	-	-	-	-	-	1	0	0	0	0	0	0	0	0	0	0
Number of resident species	5	3	5	6	6	5	4	7	4	3	4	6	5	5	7	5	4	5
Number of resident fish	11	6	10	14	17	13	10	16	15	11	16	17	17	21	19	12	13	15
Total number of fish	11	6	10	14	17	13	10	17	15	11	16	17	17	21	19	12	13	15

*: Non-resident species

Colonization history of reef number 6 continued.

Survey number:	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	to-
Weeks of colonization:	62	68	73	75	77	80	82	84	86	88	90	92	94	96	98	100	102	104	tal
Pholis laeta	-		-	-	-	-	1	0	0	0	0	0	0	0	0	0	0	0	1
Pholis sp.	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Anoplarchus purpurescens	-		-	-	-	-	-	-	-	-	-	-	-	-	1	0	0	0	1
Blennioidei spp.	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Anarrhichthys ocellatus	1		0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	3
Coryphopterus nicholsi	6		19	15	13	16	14	19	16	17	19	13	10	10	8	11	10	11	299
Sebastes auriculatus	0		0	0	0	0	0	0	0	0	0	0	0	1	2	1	2	1	9
Sebastes caurinus	2		3	3	1	3	3	1	2	3	1	1	4	0	2	2	1	2	110
Sebastes maliger	3		1	4	4	2	1	5	2	3	5	4	4	6	7	4	1	3	131
Non-schooling *S. melanops*	0		0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	12
Sebastes melanops	0		0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	12
Sebastes pinniger	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Sebastes spp.	0		1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	15
Sebastes : Total	5		4	8	6	5	4	6	5	6	6	5	8	7	11	7	4	6	265
Hexagrammos decagrammus	2		0	2	1	1	1	1	1	1	1	1	1	0	0	0	1	0	41
Artedius spp.	0		0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	4
Artedius lateralis	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Clinocottus spp.	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Hemilepidotus hemilepidotus	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Jordania zonope	0		0	0	0	1	0	0	0	1	0	0	0	0	2	0	2	1	10
Rhamphocottus richardsoni	0		0	0	0	0	0	1	0	0	0	1	0	1	1	1	1	0	8
Cottidae spp.	0		0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2
Cottidae: Total	0		0	0	0	1	0	1	0	1	0	1	0	1	3	3	5	1	29
Pleuronectidae spp.*	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Number of resident species	5		3	5	5	5	6	5	5	5	4	5	4	4	7	6	8	5	18
Number of resident fish	14		24	26	21	24	21	27	22	25	27	20	19	18	23	21	20	18	656
Total number of fish	14		24	26	21	24	21	27	22	25	27	20	19	18	23	21	20	18	657

*: Non-resident species

Colonization history of reef number 7

Survey number:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Weeks of colonization:	0	0	0	0	0	0	0	0	0	0	0	0	1	3	6	9	12	14
*Aulorhynchus flavidus**													-	-	-	-		-
*Rhacochilus vacca**													-	-	-	-		-
Pholis ornata													-	-	-	-		-
Anarrhichthys ocellatus													-	-	-	-		-
Coryphopterus nicholsi													4	8	8	17		13
Sebastes caurinus													1	1	3	0		3
Sebastes maliger													2	0	0	1		0
Non-schooling *S. melanops*													5	4	4	7		1
Sebastes melanops													5	4	4	7		1
Sebastes pinniger													-	-	-	5		2
Sebastes spp.													-	1	0	3		0
Sebastes : Total													8	5	7	13		6
Hexagrammos decagrammus													1	1	1	2		1
Ophiodon elongatus													2	0	0	0		0
Oxylebius pictus													-	-	-	-		-
Clinocottus spp.													-	-	-	-		-
Hemilepidotus hemilepidotus													-	-	-	-		-
Jordania zonope													-	-	-	-		-
Rhamphocottus richardsoni													-	-	-	-		-
Cottidae: Total													-	-	-	-		-
Number of resident species													6	4	4	5		5
Number of resident fish													15	15	16	35		20
Total number of fish													15	15	16	35		20

*: Non-resident species

Colonization history of reef number 7 continued.

Survey number:	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Weeks of colonization:	16	21	25	27	29	31	33	35	37	39	41	43	45	47	49	51	53	57
*Aulorhynchus flavidus**	-	-	-	-	-	-	-	-	-	-	5	0	0	0	0	0	0	0
*Rhacochilus vacca**	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholis ornata	-	-	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anarrhichthys ocellatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0
Coryphopterus nicholsi	5	4	13	7	9	8	6	8	13	12	13	15	16	14	18	8	15	15
Sebastes caurinus	0	1	0	0	1	0	0	2	1	3	1	1	2	2	1	3	3	3
Sebastes maliger	0	3	0	2	2	1	0	1	3	0	2	1	1	2	2	2	2	0
Non-schooling *S. melanops*	1	0	2	1	2	0	1	0	2	1	1	2	5	6	5	1	1	2
Sebastes melanops	1	0	2	1	2	0	1	0	2	1	1	2	5	6	5	1	1	2
Sebastes pinniger	3	2	2	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Sebastes spp.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0
Sebastes : Total	4	6	4	4	6	2	1	3	6	4	4	4	8	10	8	6	6	5
Hexagrammos decagrammus	0	1	0	1	0	0	2	0	0	0	0	0	1	1	1	2	2	1
Ophiodon elongatus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Oxylebius pictus	-	-	-	1	0	0	0	0	1	0	0	0	1	0	0	0	0	1
Clinocottus spp.	-	-	-	-	-	-	-	-	-	1	0	0	0	0	0	0	0	0
Hemilepidotus hemilepidotus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	0	0
Jordania zonope	-	-	-	-	1	0	0	1	1	1	2	3	2	1	3	0	3	0
Rhamphocottus richardsoni	-	-	-	-	-	-	-	-	1	0	1	0	1	0	1	0	0	0
Cottidae: Total	-	-	-	-	1	0	0	1	2	2	3	3	3	1	5	0	3	0
Number of resident species	3	5	4	6	6	3	3	4	7	5	6	6	8	6	8	5	7	5
Number of resident fish	9	11	18	13	16	10	9	12	22	19	20	23	29	26	33	16	27	22
Total number of fish	10	11	18	13	16	10	9	12	22	19	25	23	29	26	33	16	27	22

*: Non-resident species

Colonization history of reef number 7 continued.

Survey number:	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	to-
Weeks of colonization:	62	68	73	75	77	80	82	84	86	88	90	92	94	96	98	100	102	104	tal
*Aulorhynchus flavidus**	0																		5
*Rhacochilus vacca**	0																		1
Pholis ornata	0																		1
Anarrhichthys ocellatus	0																		1
Coryphopterus nicholsi	9																		258
Sebastes caurinus	1																		33
Sebastes maliger	3																		30
Non-schooling *S. melanops*	2																		56
Sebastes melanops	2																		56
Sebastes pinniger	0																		17
Sebastes spp.	0																		6
Sebastes : Total	5																		136
Hexagrammos decagrammus	1																		19
Ophiodon elongatus	0																		3
Oxylebius pictus	1																		5
Clinocottus spp.	0																		1
Hemilepidotus hemilepidotus	0																		1
Jordania zonope	1																		19
Rhamphocottus richardsoni	0																		4
Cottidae: Total	1																		25
Number of resident species	7																		14
Number of resident fish	18																		454
Total number of fish	18																		460

*: Non-resident species

Colonization history of reef number 8

Survey number:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Weeks of colonization:	0	0	0	0	0	0	0	0	0	0	0	0	1	3	6	9	12	14
Gobiesox maeandricus													-	-	-	-	-	-
*Brachyistius frenatus**													-	-	-	-	-	-
*Rhacochilus vacca**													-	1	0	0	0	0
Chirolophis decoratus													-	-	-	-	-	-
Anarrhichthys ocellatus													-	1	0	0	0	0
Coryphopterus nicholsi													14	10	13	13	7	7
Sebastes caurinus													1	1	3	4	2	1
Sebastes maliger													-	-	-	-	-	-
Non-schooling *S. melanops*													1	1	1	5	1	3
Schooling *S.melanops**													-	-	-	-	-	-
Sebastes melanops													1	1	1	5	1	3
Sebastes mystinus													-	-	-	-	-	-
Sebastes pinniger													-	-	-	-	-	1
Sebastes spp.													1	0	0	0	0	0
Sebastes: Total													2	2	3	9	3	5
Hexagrammos decagrammus													2	1	2	3	0	2
Ophiodon elongatus													-	-	-	-	-	-
Oxylebius pictus													-	-	-	-	-	-
Artedius lateralis													-	-	-	-	-	-
Jordania zonope													-	-	-	-	-	-
Rhamphocottus richardsoni													-	-	-	-	-	-
Cottidae: Total													-	-	-	-	-	-
Pleuronectidae spp.*													-	-	-	-	-	-
Number of resident species													4	5	4	4	3	5
Number of resident fish													19	14	18	25	10	14
Total number of fish													19	15	18	25	10	14

*: Non-resident species

Colonization history of reef number 8 continued.

Survey number:	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Weeks of colonization:	16	21	25	27	29	31	33	35	37	39	41	43	45	47	49	51	53	57
Gobiesox maeandricus	-	-	-	-	-	-	1	0	0	0	0	0	0	0	0	0	0	0
*Brachyistius frenatus**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
*Rhacochilus vacca**	0	0	0	0	0	0	0	0	0	0	0	0	0	[illegible]	0	0	0	0
Chirolophis decoratus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Anarrhichthys ocellatus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coryphopterus nicholsi	7	5	3	6	9	6	5	2	4	12	17	19	25	40	30	25	16	15
Sebastes caurinus	1	3	0	0	2	2	1	1	1	0	0	1	0	0	0	1	0	0
Sebastes maliger	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Non-schooling *S. melanops*	0	0	0	1	0	0	0	0	0	0	0	4	1	6	7	7	7	9
Schooling *S.melanops**	-	-	-	-	-	-	-	-	-	-	-	-	-	25	20	0	0	0
Sebastes melanops	0	0	0	1	0	0	0	0	0	0	0	4	1	31	27	7	7	9
Sebastes mystinus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6
Sebastes pinniger	3	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1
Sebastes spp.	0	0	1	1	0	1	1	0	0	0	0	0	1	0	0	0	0	3
Sebastes : Total	4	4	0	1	3	2	1	1	1	0	0	5	1	31	28	8	8	16
Hexagrammos decagrammus	1	0	0	1	1	0	0	1	0	2	1	0	1	3	4	2	1	0
Ophiodon elongatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	0
Oxylebius pictus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	0	0
Artedius lateralis	-	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jordania zonope	-	-	-	1	3	0	1	1	2	1	1	2	2	3	1	3	0	4
Rhamphocottus richardsoni	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cottidae: Total	-	1	0	1	3	0	1	1	2	1	1	2	2	3	1	3	0	4
Pleuronectidae spp.*	-	-	-	-	-	-	-	1	0	0	0	1	0	0	0	0	0	0
Number of resident species	4	4	2	5	5	2	5	4	3	3	3	4	5	4	6	6	4	5
Number of resident fish	12	10	5	10	16	9	9	5	7	15	19	26	30	52	44	39	25	38
Total number of fish	12	10	5	10	16	9	9	6	7	15	19	27	30	77	64	39	25	38

*: Non-resident species

Colonization history of reef number 8 continued.

Survey number:	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	to-
Weeks of colonization:	62	68	73	75	77	80	82	84	86	88	90	92	94	96	98	100	102	104	tal
Gobiesox maeandricus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2
Brachyistius frenatus†	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Rhacochilus vacca†	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Chirolophis decoratus	-	-	-	-	-	-	-	-	-	-	-	1	0	0	0	0	0	0	1
Anarrhichthys ocellatus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	4
Coryphopterus nicholsi	8	12	19	16	21	6	13	14	13	9	13	10	27	25	21	20	35	18	610
Sebastes caurinus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	26
Sebastes maliger	-	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	4
Non-schooling *S. melanops*	11	2	7	4	10	0	2	0	0	0	4	0	1	0	0	4	5	4	108
Schooling *S.melanops*†	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	45
Sebastes melanops	11	2	7	4	10	0	2	0	0	0	4	0	1	0	0	4	5	4	153
Sebastes mystinus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7
Sebastes pinniger	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9
Sebastes spp.	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	10
Sebastes : Total	12	4	7	4	10	0	2	0	0	0	4	0	1	1	1	5	6	4	199
Hexagrammos decagrammus	2	1	1	1	0	0	2	1	0	1	0	0	2	1	2	0	0	1	43
Ophiodon elongatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Oxylebius pictus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Artedius lateralis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Jordania zonope	2	0	2	1	2	1	2	2	4	3	2	2	3	4	8	6	6	4	79
Rhamphocottus richardsoni	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	0	0	0	1
Cottidae: Total	2	0	2	1	2	1	2	2	4	3	2	2	3	5	8	6	6	4	81
Pleuronectidae spp.*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Number of resident species	5	5	4	4	3	3	4	3	2	3	3	3	5	5	4	5	4	4	15
Number of resident fish	24	17	29	22	33	9	19	17	17	13	19	13	34	32	32	32	47	27	907
Total number of fish	27	17	29	22	33	9	19	17	17	13	19	13	34	32	32	32	47	27	958

†: Non-resident species

Colonization history of reef number 9

Survey number:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Weeks of colonizatton:	0	0	0	0	0	0	0	0	0	0	0	0	1	3	6	9	12	14
*Rhacochilus vacca**													-	1	0	0	0	0
Anoplarchus purpurescens													-	-	-	-	-	-
Coryphopterus nicholsi													17	11	15	13	10	7
Sebastes caurinus													-	-	1	2	2	1
Sebastes maliger													-	-	-	-	1	1
Non-schooling *S. melanops*													9	4	5	8	3	5
Schooling *S.melanops**													-	6	0	0	0	0
Sebastes melanops													9	10	5	8	3	5
Sebastes pinniger													-	-	-	2	8	6
Sebastes spp.													-	-	-	7	0	0
Sebastes : Total													9	10	6	12	14	13
Hexagrammos decagrammus													2	2	2	1	0	1
Oxylebius pictus													-	-	-	-	-	-
Artedius spp.													-	-	-	-	-	-
Clinocottus spp.													-	-	-	-	-	-
Jordania zonope													-	-	-	-	-	-
Cottidae spp.													-	-	-	-	-	-
Cottidae: Total													-	-	-	-	-	-
*Lepidopsetta bilineata**													-	-	-	-	-	-
Number of resident species													3	3	4	5	5	6
Number of resident fish,													28	17	23	33	24	21
Total number of fish													28	24	23	33	24	21

*: Non-resident species

Colonization history of reef number 9 continued.

Survey number:	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Weeks of colonization:	16	21	25	27	29	31	33	35	37	39	41	43	45	47	49	51	53	57
*Rhacochilus vacca**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anoplarchus purpurescens	-	-	-	-	-	-	1	0	0	0	0	0	0	0	0	0	0	0
Coryphopterus nicholsi	6	2	2	4	9	6	4	6	9	11	14	20	14	21	20	19	24	15
Sebastes caurinus	1	1	2	1	0	2	1	1	2	1	1	1	1	1	2	2	0	2
Sebastes maliger	2	0	0	1	3	1	0	1	1	2	0	2	0	0	2	0	1	2
Non-schooling *S. melanops*	0	0	1	2	3	1	0	1	0	0	0	5	0	1	10	8	2	2
Schooling *S.melanops**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	26
Sebastes melanops	0	0	1	2	3	1	0	1	0	0	0	5	0	1	10	8	2	28
Sebastes pinniger	11	1	1	1	0	2	1	1	2	1	1	1	0	0	0	0	0	0
Sebastes spp.	0	1	1	2	0	1	1	0	1	0	2	0	0	0	0	0	0	5
Sebastes : Total	14	2	4	5	6	6	2	4	5	4	2	9	1	2	14	10	3	32
Hexagrammos decagrammus	1	1	0	0	0	1	0	0	0	3	2	0	0	1	1	1	1	1
Oxylebius pictus	-	-	-	-	-	-	-	-	-	-	1	0	0	1	0	0	0	0
Artedius spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	0	0	0
Clinocottus spp.	-	-	-	-	-	1	0	0	0	0	0	0	0	0	1	0	0	2
Jordania zonope	-	-	-	-	-	1	0	0	0	1	1	2	1	1	2	2	0	3
Cottidae spp.	-	-	-	-	-	-	-	-	-	-	1	0	1	0	0	0	0	0
Cottidae: Total	-	-	-	-	-	2	0	0	0	1	2	2	2	2	4	2	0	5
*Lepidopsetta bilineata**	-	-	-	-	-	1	0	0	0	0	0	0	0	0	0	0	0	0
Number of resident species	5	4	4	5	3	8	4	5	4	6	7	6	3	7	8	5	4	7
Number of resident fish	21	6	7	11	15	16	8	10	15	19	23	31	17	27	39	32	28	32
Total number of fish	21	6	7	11	15	17	8	10	15	19	23	31	17	27	39	32	28	58

*: Non-resident species

Colonization history of reef number 9 continued.

Survey number:	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	to-
Weeks of colonization:	62	68	73	75	77	80	82	84	86	88	90	92	94	96	98	100	102	104	tal
*Rhacochilus vacca**	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	1
Anoplarchus purpurescens	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	1
Coryphopterus nicholsi	17	8	9	9	13	7	13	18	9	6	11		17	24	29	22	25	32	548
Sebastes caurinus	0	0	0	0	0	0	1	1	0	0	0		0	1	2	2	1	1	37
Sebastes maliger	5	2	1	0	0	0	2	0	0	0	2		2	2	1	5	1	1	44
Non-schooling *S. melanops*	6	2	5	3	2	1	1	1	0	1	2		0	1	2	6	6	7	116
Schooling *S.melanops**	20	8	6	0	0	0	0	0	0	0	0		0	0	0	0	0	0	66
Sebastes melanops	26	10	11	3	2	1	1	1	0	1	2		0	1	2	6	6	7	182
Sebastes pinniger	0	0	3	0	0	0	0	0	0	0	0		0	0	0	0	0	0	42
Sebastes spp.	0	0	0	0	0	0	1	1	0	0	0		0	0	0	2	0	0	25
Sebastes : Total	31	12	15	3	2	1	4	2	0	1	4		2	4	5	13	8	9	305
Hexagrammos decagrammus	2	2	1	1	2	0	1	1	1	1	2		1	1	0	1	1	1	40
Oxylebius pictus	1	1	0	0	0	0	0	0	0	0	0		0	1	0	0	0	0	5
Artedius spp.	0	0	0	1	0	0	0	0	0	0	0		0	0	0	1	0	0	4
Clinocottus spp.	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	4
Jordania zonope	0	1	1	2	1	1	1	0	2	1	1		0	4	9	7	9	7	61
Cottidae spp.	0	0	0	0	0	0	0	0	0	0	0		0	0	0	2	1	1	6
Cottidae: Total	0	1	1	3	1	1	1	0	2	1	1		0	4	9	10	10	8	75
*Lepidopsetta bilineata**	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	1
Number of resident species	5	6	6	5	4	3	6	4	3	4	5		3	7	5	7	6	6	11
Number of resident fish	31	16	20	16	18	9	20	22	12	9	18		20	34	43	48	44	50	933
Total number of fish	51	24	26	16	18	9	20	22	12	9	18		20	34	43	48	44	50	1001

*: Non-resident species

Colonization history of reef number 10

Survey number:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Weeks of colonization:	0	0	0	0	0	0	0	0	0	0	0	0	1	3	6	9	12	14
Anarrhichthys ocellatus													1	0	0	0	0	0
Coryphopterus nicholsi													5	9	5	5	2	4
Sebastes caurinus													1	1	2	3	4	2
Sebastes maliger													-	1	0	1	0	4
Non-schooling *S. melanops*													2	11	9	7	6	10
Schooling *S.melanops**													-	12	20	8	0	0
Sebastes melanops													2	23	29	15	6	10
Sebastes pinniger													-	-	-	5	7	19
Sebastes spp.													-	-	2	9	0	0
Sebastes : Total													3	25	31	24	17	35
Hexagrammos decagrammus													2	2	0	1	2	2
Artedius spp.													-	-	-	-	-	-
Jordania zonope													-	-	-	-	-	-
Cottidae spp.													-	-	-	-	-	-
Cottidae: Total													-	-	-	-	-	-
Number of resident species													5	5	3	6	5	6
Number of resident fish													11	24	18	31	21	41
Total number of fish													11	36	38	39	21	41

*: Non-resident species

Colonization history of reef number 10 continued..

Survey number:	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Weeks of colonization:	16	21	25	27	29	31	33	35	37	39	41	43	45	47	49	51	53	57
Anarrhichthys ocellatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Coryphopterus nicholsi	6	2	0	2	7	5	3	3	3	16	12	14	8	20	10	21	17	18
Sebastes caurinus	1	1	0	3	3	6	3	2	1	3	5	5	4	2	2	2	2	5
Sebastes maliger	5	0	0	4	0	2	2	2	0	1	3	4	2	2	2	0	0	0
Non-schooling *S. melanops*	6	1	1	2	3	5	2	1	0	1	2	3	2	11	3	12	3	8
Schooling *S.melanops**	0	0	0	0	0	0	0	0	0	0	0	0	0	81	50	0	0	6
Sebastes melanops	6	1	1	2	3	5	2	1	0	1	2	3	2	92	53	12	3	14
Sebastes pinniger	15	3	1	1	2	0	0	0	0	1	1	0	0	0	0	0	0	2
Sebastes spp.	2	1	1	0	1	0	1	4	2	0	1	0	0	0	0	1	0	0
Sebastes : Total	27	5	2	10	8	13	7	5	1	6	11	12	8	96	57	14	5	21
Hexagrammos decagrammus	2	0	1	2	1	1	2	0	0	0	1	0	0	1	2	2	2	0
Artedius spp.	-	-	-	-	-	-	-	-	-	1	0	1	0	0	0	0	0	0
Jordania zonope	-	-	-	-	-	-	1	1	0	1	1	1	1	1	0	1	0	0
Cottidae spp.	-	-	-	-	-	-	-	-	-	-	1	0	0	0	0	0	0	0
Cottidae: Total	-	-	-	-	-	-	1	1	0	2	2	2	1	1	0	1	0	0
Number of resident species	6	4	3	6	5	5	6	5	2	7	7	6	5	6	5	6	5	4
Number of resident fish	37	8	4	14	17	19	14	13	6	24	27	28	17	37	19	40	25	33
Total number of fish	37	8	4	14	17	19	14	13	6	24	27	28	17	118	69	40	25	39

*: Non-resident species

Colonization history of reef number 10 continued.

Survey number:	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	to-
Weeks of colonization:	62	68	73	75	77	80	82	84	86	88	90	92	94	96	98	100	102	104	tal
Anarrhichthys ocellatus	0	0																	3
Coryphopterus nicholsi	4	11																	212
Sebastes caurinus	0	0																	63
Sebastes maliger	0	0																	35
Non-schooling *S. melanops*	7	10																	128
Schooling *S.melanops**	0	0																	177
Sebastes melanops	7	10																	305
Sebastes pinniger	2	1																	60
Sebastes spp.	0	0																	25
Sebastes : Total	9	11																	463
Hexagrammos decagrammus	3	0																	29
Artedius spp.	0	0																	2
Jordania zonope	1	0																	9
Cottidae spp.	0	0																	1
Cottidae: Total	1	0																	12
Number of resident species	5	3																	9
Number of resident fish	17	22																	567
Total number of fish	17	22																	744

*: Non-resident species

Colonization history of reef number 11

Survey number:	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	to-
Weeks of colonization:	0	0	0	0	0	0	2	4	6	8	10	12	14	16	18	20	22	24	tal
Coryphopterus nicholsi							-	-	2	4	7	4	3	7	4	7	6	3	47
Sebastes auriculatus							-	-	-	1	1	0	0	0	0	0	0	0	2
Sebastes caurinus							-	-	-	-	-	-	-	-	2	0	1	1	4
Sebastes maliger							-	-	-	-	-	-	-	-	-	1	0	0	1
Non-schooling *S. melanops*							-	-	-	-	-	-	-	1	0	0	9	12	22
Schooling *S.melanops**							-	-	-	-	-	-	-	-	-	-	100	100	200
Sebastes melanops							-	-	-	-	-	-	-	1	0	0	109	112	222
Sebastes pinniger							-	-	-	-	-	-	1	0	0	0	2	0	3
Sebastes spp.							-	-	-	-	-	-	-	-	-	-	-	1	1
Sebastes : Total							-	-	-	1	1	0	1	1	2	1	112	113	232
Hexagrammos decagrammus							1	0	0	1	0	0	1	1	0	1	0	1	6
Ophiodon elongatus							-	-	1	0	0	0	0	0	1	1	1	1	5
Clinocottus spp.							-	-	-	-	-	-	-	-	-	1	0	0	1
Jordania zonope							-	-	-	1	1	0	2	1	3	3	5	2	18
Cottidae spp.							-	-	-	-	-	-	-	1	0	0	0	0	1
Cottidae: Total							-	-	-	1	1	0	2	2	3	4	5	2	20
Number of resident species							1	0	2	4	3	1	4	4	4	6	6	6	10
Number of resident fish							1	0	3	7	9	4	7	11	10	14	24	21	111
Total number of fish							1	0	3	7	9	4	7	11	10	14	124	121	311

*: Non-resident species

Colonization history of reef number 12

Survey number:	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	to-
Weeks of colonization:	0	0	0	0	0	0	2	4	6	8	10	12	14	16	18	20	22	24	tal
Coryphopterus nicholsi							1	4	2	4	5	4	5	4	4	3	8	3	47
Sebastes caurinus							1	0	0	0	0	0	0	1	1	0	1	2	6
Sebastes maliger							-	-	1	0	1	0	1	0	0	0	0	0	3
Non-schooling *S. melanops*							3	1	0	1	0	0	1	0	0	0	10	10	26
Schooling *S.melanops**							-	-	-	-	-	-	-	-	-	-	15	20	35
Sebastes melanops							3	1	0	1	0	0	1	0	0	0	25	30	61
Sebastes pinniger							-	-	-	1	0	0	0	0	0	0	0	2	3
Sebastes spp.							-	1	1	0	0	0	0	0	0	1	0	0	3
Sebastes : Total							4	1	1	2	1	0	2	1	1	0	26	34	73
Hexagrammos decagrammus							-	-	1	1	0	0	0	0	0	0	1	0	3
Artedius spp.							-	-	-	1	1	2	1	0	1	2	1	1	10
Enophrys bison							-	-	-	-	-	-	1	1	0	0	0	0	2
Jordania zonope							-	-	-	2	0	1	0	1	4	2	5	5	20
Cottidae spp.							-	-	-	-	-	-	-	-	1	0	0	1	2
Cottidae: Total							-	-	-	3	1	3	2	2	6	4	6	7	34
Number of resident species							3	3	4	6	3	3	4	3	4	3	6	6	8
Number of resident fish							5	6	5	10	7	7	8	6	11	8	26	24	123
Total number of fish							5	6	5	10	7	7	9	7	11	8	41	44	160

*: Non-resident species

Colonization history of reef number 13

Survey number:	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	to-
Weeks of colonization:	0	0	0	0	0	0	2	4	6	8	10	12	14	16	18	20	22	24	tal
Pholis sp.							-	-	-	-	-	-	-	1	0	0	0	0	1
Coryphopterus nicholsi							1	1	1	3	4	3	1	1	2	4	4	4	29
Sebastes auriculatus							-	-	-	1	0	0	0	0	0	0	0	0	1
Sebastes caurinus							-	-	-	-	1	1	1	1	0	1	0	0	5
Sebastes maliger							-	-	-	-	1	0	0	0	0	0	0	0	1
Sebastes pinniger							-	-	1	1	0	0	0	0	0	0	0	0	2
Sebastes : Total							-	-	1	2	2	1	1	1	0	1	0	0	9
Hexagrammos decagrammus							-	-	-	1	1	0	1	0	2	0	0	0	5
Artedius spp.							-	-	-	-	-	-	1	0	0	1	1	0	3
Rhamphocottus richardsoni							-	-	-	-	-	-	-	-	-	-	-	1	1
Cottidae: Total							-	-	-	-	-	-	1	0	0	1	1	1	4
Number of resident species							1	1	2	4	4	2	4	3	2	3	2	2	9
Number of resident fish							1	1	2	6	7	4	4	3	4	6	5	5	48
Total number of fish							1	1	2	6	7	4	4	3	4	6	5	5	48

*: Non-resident species

Colonization history of reef number 14

Survey number:	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	to-
Weeks of colonization:	0	0	0	0	0	0	2	4	6	8	10	12	14	16	18	20	22	24	tal
Anarrhichthys ocellatus							-	-	-	-	-	-	-	-	-	1	1	0	2
Coryphopterus nicholsi							-	-	-	-	-	-	-	2	1	0	4	4	11
Sebastes auriculatus							-	-	-	-	-	-	-	-	-	1	0	0	1
Sebastes caurinus							-	-	-	-	-	-	-	-	1	0	2	1	4
Non-schooling *S. melanops*							-	-	-	-	-	-	-	-	-	-	-	1	1
Sebastes melanops							-	-	-	-	-	-	-	-	-	-	-	1	1
Sebastes spp.							-	-	-	-	-	-	-	-	-	1	0	1	2
Sebastes : Total							-	-	-	-	-	-	-	-	1	1	2	2	6
Hexagrammos decagrammus							-	-	-	-	-	-	-	1	1	0	0	0	2
Artedius spp.							-	-	-	-	-	-	-	-	1	1	1	0	3
Jordania zonope							1	0	0	0	0	0	0	0	0	2	3	2	8
Rhamphocottus richardsoni							-	-	-	-	-	1	0	0	1	0	0	0	2
Cottidae spp.							-	-	-	-	-	-	-	-	2	0	0	0	2
Cottidae: Total							1	0	0	0	0	1	0	0	4	3	4	2	15
*Agonopsis emmelane**							-	-	-	-	-	-	-	-	-	-	-	1	1
Number of resident species							1	0	0	0	0	1	0	2	5	5	5	5	10
Number of resident fish							1	0	0	0	0	1	0	3	7	6	11	10	39
Total number of fish							1	0	0	0	0	1	0	3	7	6	11	10	39

*: Non-resident species

Colonization history of reef number 15

Survey number:	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	to-
Weeks of colonization:	0	0	0	0	0	0	2	4	6	8	10	12	14	16	18	20	22	24	tal
Anoplarchus purpurescens							-	-	-	-	-	-	-	1	0	0	0	0	1
Coryphopterus nicholsi							3	3	4	3	4	3	3	4	3	4	4	3	41
Sebastes maliger							-	1	0	1	0	1	1	1	0	0	1	1	7
Sebastes : Total							-	1	0	1	0	1	1	1	0	0	1	1	7
Hexagrammos decagrammus							-	-	-	1	0	0	0	1	0	0	0	2	4
Artedius spp.							-	-	-	-	1	0	1	1	2	2	2	2	11
Jordania zonope							-	-	-	1	1	1	0	2	3	3	2	1	14
Rhamphocottus richardsoni							-	-	-	-	-	-	-	-	1	0	0	0	1
Cottidae: Total							-	-	-	1	2	1	1	3	6	5	4	3	26
Number of resident species							1	2	1	4	3	3	3	6	4	3	4	5	7
Number of resident fish							3	4	4	6	6	5	5	10	9	9	9	9	79
Total number of fish							3	4	4	6	6	5	5	10	9	9	9	9	79

*: Non-resident species

Colonization history of reef number 16

Survey number:	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	to-
Weeks of colonization:	0	0	0	0	0	0	2	4	6	8	10	12	14	16	18	20	22	24	tal
Sebastes auriculatus							-	-	-	-	-	-	-	-	-	1	2	0	3
Sebastes caurinus							-	-	-	-	-	-	-	-	-	1	0	0	1
Sebastes maliger							-	-	-	-	-	-	-	1	1	1	1	1	5
Sebastes spp.							-	-	-	-	-	-	1	0	0	0	0	0	1
Sebastes : Total							-	-	-	-	-	-	-	1	1	3	3	1	9
Hexagrammos decagrammus							-	-	-	-	-	-	-	-	1	1	1	0	3
Artedius spp.							-	-	-	-	-	-	1	1	1	1	1	1	6
Rhamphocottus richardsoni							-	-	-	-	-	-	-	-	-	-	1	0	1
Cottidae spp.							-	-	-	-	-	-	-	-	2	1	0	0	3
Cottidae: Total							-	-	-	-	-	-	1	1	3	2	2	1	10
Number of resident species							-	-	-	-	-	-	1	2	3	5	5	2	6
Number of resident fish							-	-	-	-	-	-	2	2	5	6	6	2	23
Total number of fish							-	-	-	-	-	-	2	2	5	6	6	2	23

*: Non-resident species

Colonization history of reef number 17

Survey number:	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	to-
Weeks of colonization:	0	0	0	0	0	0	2	4	6	8	10	12	14	16	18	20	22	24	tal
Chirolophis decoratus							-	-	-	-	-	-	-	-	-	2	1	0	3
Coryphopterus nicholsi							2	5	9	9	11	5	7	6	5	5	5	4	73
Sebastes auriculatus							-	-	-	-	-	-	-	-	-	1	0	0	1
Sebastes : Total							-	-	-	-	-	-	-	-	-	1	0	0	1
Hexagrammos decagrammus							-	-	-	-	-	-	-	1	1	0	0	1	3
Artedius spp.							-	-	1	0	1	0	2	1	2	4	4	2	17
Clinocottus spp.							1	0	0	1	0	1	0	0	0	0	0	0	3
Jordania zonope							-	1	0	1	0	2	1	3	4	1	3	3	19
Cottidae spp.							-	-	-	-	-	-	1	0	0	0	0	0	1
Cottidae: Total							1	1	1	2	1	3	4	4	6	5	7	5	40
*Lepidopsetta bilineata**							-	-	-	-	1	0	0	0	0	0	0	0	1
Number of resident species							2	2	2	3	2	3	3	4	4	5	4	4	7
Number of resident fish							3	6	10	11	12	8	11	11	12	13	13	10	120
Total number of fish							3	6	10	11	13	8	11	11	12	13	13	10	121

*: Non-resident species

Colonization history of reef number 18

Survey number:	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	to-
Weeks of colonization:	0	0	0	0	0	0	2	4	6	8	10	12	14	16	18	20	22	24	tal
Coryphopterus nicholsi							3	9	9	11	13	8	6	2	2	4	5	3	75
Sebastes auriculatus							-	-	-	2	0	0	0	0	0	0	0	0	2
Sebastes caurinus							-	-	-	-	-	-	-	-	-	-	-	1	1
Sebastes spp.							-	-	-	-	1	0	0	0	0	0	0	0	1
Sebastes : Total							-	-	-	2	0	0	0	0	0	0	0	1	3
Hexagrammos decagrammus							-	-	-	1	0	0	0	1	0	0	0	0	2
Artedius spp.							-	-	-	-	-	1	0	2	1	1	1	1	7
Clinocottus spp.							-	-	-	-	-	-	1	0	0	0	0	0	1
Jordania zonope							-	-	-	-	-	-	-	-	-	1	1	2	4
Cottidae spp.							-	-	-	-	-	-	-	1	0	0	0	1	2
Cottidae: Total							-	-	-	-	-	1	1	3	1	2	2	4	14
Number of resident species							1	1	1	3	1	2	2	3	2	3	3	4	7
Number of resident fish							3	9	9	14	14	9	7	6	3	6	7	8	95
Total number of fish							3	9	9	14	14	9	7	6	3	6	7	8	95

*: Non-resident species

D. Appendix IV: Chi-square tests for the space utilization on the transects

The vertical bars indicate the categories that were pooled together for the tests. For the definition of the microhabitat categories (position and substratum), see page 31.

Microhabitat Categories	Sampling Periods J-M	A-J	J-S	O-D
Coryphopterus nicholsi				
Rock, in a hole	163	234	296	69
Rock, exposed	777	2072	3887	363
Rock, swimming	0	14	21	0
Sand, in a hole	107	701	97	19
Sand, exposed	225	116	923	75
Sand, swimming	0	1	1	0
X^2, 1355.52; df, 12.				
Hexagrammos decagrammus				
Rock, in a hole	4	5	1	1
Rock, exposed	6	30	46	1
Rock, swimming	6	18	69	11
Sand, exposed	4	4	29	3
Sand, swimming	1	1	12	0
X^2, 40.52; df, 9.				
Sebastes melanops				
Rock, in a hole	7	31	29	6
Rock, exposed	8	6	5	1
Rock, swimming	6	16	161	8
Sand, in a hole	2	0	1	0
Sand, swimming	1	1	5	1
X^2, 14.02; df, 6.				
Sebastes caurinus				
Rock, in a hole	17	21	11	5
Rock, exposed	1	10	43	1
Rock, swimming	0	1	21	2
Sand, in a hole	2	0	1	0
Sand, exposed	0	0	3	0
X^2, 24.22; df, 6.				
Sebastes maliger				
Rock, in a hole	51	9	4	10
Rock, exposed	28	11	3	31
Rock, swimming	26	5	4	18
X^2, 19.08; df, 6.				

E. Appendix V: Tagging results

Fish	Length (mm)	Date tagged	Date last seen	Length of residence
C. nicholsi	91	25/7/79	11/3/80	231
C. nicholsi	82	25/7/79	11/2/80	202
S. maliger	77	22/6/79	31/10/79	111
S. maliger	79	27/6/79	5/2/80	229
S. maliger	135	24/7/79	24/7/79	0
S. maliger	60	24/7/79	24/7/79	0
S. maliger	88	25/7/79	16/8/79	56
S. caurinus	89	22/6/79	2/7/80	382
S. caurinus	94	22/6/79	12/3/80	265
S. melanops	126	22/6/79	29/8/79	69
J. zonope	88	27/6/79	25/1/80	213

Summary of the tagging done on reef no. 4.

Species	no.	Mean duration of stay (in days).	Range
C. nicholsi	2	216	202-231
J. zonope	1	213	
S. melanops	1	69	
S. caurinus	2	274	382-265
S. maliger	5	99	0-229